SEDIMENTOLOGICAL, ECOLOGICAL AND HYDRODYNAMIC EFFECTS OF A TUBE-BUILDING POLYCHAETE (LANICE CONCHILEGA PALLAS)

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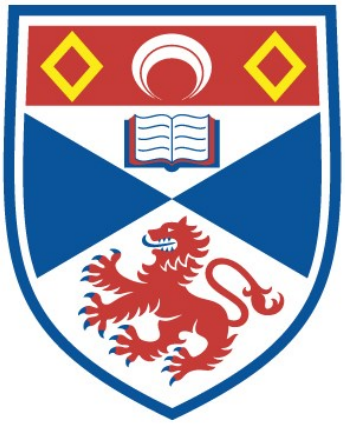
A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



1983

Abstract

A tidal channel habitat dominated numerically by the tube-building polychaete Lanice conchilega is described from Tentsmuir Beach in N.E. Fife, Scotland. This habitat was named the Lanice tidal channel sub-environment and was characterized by sedimentological features and macrofauna associated with aggregations of Lanice. These aggregations formed a habitat structurally and faunistically more heterogeneous than surrounding mobile sand habitats. The aggregations occurred in discrete areas protected by a linear sand bar from onshore swell but were subjected to relatively strong tidal currents.

Eight divisions of the sub-environment were described from surface features and used to compare sediment and macrofauna distribution in relation to environmental features. The dense tube beds provided a stable substratum for settlement and growth of algal species. Mounds and stable flats were produced during the spring by sediment deposition combined with rapid growth of algal thalli and tube extension. The structures were quickly eroded after the death of the algae although some areas maintained high tube densities.

The average sediment of Tentsmuir was a fine sand with a moderately well-sorted, negative-skewed, mesokurtic grain size distribution. This average distribution included a coarse tail, primarily composed of carbonate fragments. This coarse tail was concentrated in the areas numerically dominated by Lanice conchilega.

Two faunal assemblages were recognized: a shallow-sand association not strongly associated with Lanice density (Nephtys caeca, Tellina tenuis, Ophelia limacina and Donax vittatus), and a Lanice conchilega association (Lanice conchilega, Eumida sanguinea, Anaitides maculata, Harmothoë lunulata).

The effect of the projecting tubes of Lanice on particle flux in the benthic boundary layer was studied in laboratory flume experiments. Experiments were performed with dye and denatured egg albumen particles to determine flow patterns and net particle movement in individual tube wakes. Projecting tubes produced characteristic vortex patterns which may increase resuspension of sediment particles. The characteristic vortex patterns were not strongly dependent on obstacle shape or flow regime and resulted in pronounced upward motion of fluid from the bed. Particle velocities within the wake were found to be lower than ambient channel flow velocity. It is suggested that Lanice can utilize this flow disturbance to feed on resuspended food particles.

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A Thesis presented for the degree of

Doctor of Philosophy

University of St. Andrews
St. Andrews

1982

SUPERVISOR'S CERTIFICATE

I certify that Drew A. Carey has fulfilled the conditions laid down under Ordinance General No. 12 and Resolution of the University Court 1967, No. 1, of the University of St Andrews and is accordingly qualified to submit this thesis for the degree of Doctor of Philosophy.

DECLARATION

I declare that the work reported in this thesis is my own and has not been submitted for any other degree.

CURRICULUM VITAE

I graduated from The Evergreen State College, Olympia, Washington in 1976 with a B.Sc. in Geology and Marine Biology. The work described in this thesis was carried out between October, 1977 and December, 1980.

Acknowledgements

This work was supported by grants from Conoco Ltd. and the University of St Andrews. Many people lent considerable help at every stage. Roland Jack, Hugh Forbes and Charles Roemmele provided technical assistance and field support. Frank Cooper, David Ganz and Isabel Guy bravely planted worms, Dr J.A. Charlton assisted with the design and R. Jack assisted in installation of the flume. Jim Allan printed all the figures and Isabel Guy and Nancy Wood helped immeasureably with the final production.

I would like to especially thank Dr A.R. MacGregor, and Professors E.K. Walton and M.S. Laverack for providing support and facilities and Drs A.D.D. Craik, A. Okubo and H. Bokuniewicz for helpful discussions on hydrodynamics.

No stage of this project would have been possible without the continuous support and encouragement of my parents.

CONTENTS

1 Chapter 1 Introduction

1.1 Aim

The aim of this thesis was to present an integrated view of a distinct intertidal habitat, both from the perspective of the structure of the substratum and from the perspective of the animal community inhabiting this substratum. This habitat was a small portion of a secondary tidal channel of the Tay Estuary. The habitat was distinct because of the presence of a dense assemblage of the tube-building polychaete worm, Lanice conchilega (Pallas 1766). My main objective, therefore, was to examine the effect of this dense assemblage on sediment and community structure. For practical reasons I limited my investigation to the intertidal exposures of this habitat. This type of intertidal exposure (dense Lanice beds exposed to strong tidal currents) has not been described previously, either in terms of sediment distribution and structure or animal distribution and community structure. For this reason a large amount of purely descriptive detail has been included. I hope that some of the more peripheral information will provide a starting point for further investigations of the Tentsmuir tidal channel environment.

Although an integrated description was the main priority, one particular aspect of the habitat, the influence of the projecting tubes of Lanice on particle transport, has received additional attention. I present this aspect with the premise that water movement was a major factor influencing the development of the habitat. My aim in this additional investigation was to establish whether there was any fundamental mechanism

associated with the flow disturbance created by a single tube projecting into unidirectional flow. Thus, my aim in this part of the thesis was to describe what I perceived to be one basic unit of the entire complex of animal-sediment-flow interactions in the tube-building polychaete assemblage.

1.2 Approach

Premises

1. Sediment type is developed in response to hydrodynamic regime and particle availability.
2. Benthic organisms are adapted to the hydrodynamic regime in which they live, including sediment type.
3. Organisms can and do modify the hydrodynamic regime and the nature of the sediment (e.g. seagrass beds, reefs, mucoidal binding, bioturbation, faecal production).

This study was concerned with examination of three major components of the marine benthic environment: sediment, macrofauna and water motion.

To highlight the dynamic balance that exists between these components the area selected for study included three important features: predictable currents of moderate strength with minimal interference from wave action, small variation in sediment type and supply over a wide area, abundant macrofaunal organisms capable of modifying both sediment structure and the near-bottom hydrodynamic regime.

The approach in the study has been one of careful field observations of sediment structure and movement (internal structures and surface bedforms), and macrofaunal distribution with particular attention to the changes in time (tidal and seasonal scales). The investigation was followed by laboratory experiments designed to reproduce, under controlled conditions, the factor most difficult to observe in the field: the movement of water and sediment near the substratum.

2 Chapter 2 Environment and field methods

2.1 Environment

Recent excellent reviews of coastal sedimentary environments, and the resultant characteristic lithified strata, group clastic shorelines into: deltas, beaches and barrier islands, estuaries, tidal flats, and sublittoral shelf deposits (Reineck and Singh 1975, Klein 1977, Davis 1978, Reading 1978, Selley 1978, Walker 1979). It is difficult however to distinguish clearly a portion of one of these environments without some knowledge of the surrounding or adjacent portions, and this is often particularly difficult to do in lithified strata where areal information is limited or expensive to obtain.

A facies, as used here, is a description of a body of rock or the body itself which can delineate changes in the lithology, palaeontology or appearance of the rock units (see Middleton 1978 and Reading 1978). A facies is not necessarily limited to a specific rock unit. The definition should be objective and based on the observed aspect of rocks which can be used to interpret the environment of deposition (Teichert 1958). It is valid, on the one hand, to describe a facies of an ancient rock unit and the presumed environment, or on the other hand to describe a modern environment and the presumed facies that might result from deposition in the environment. To quote Teichert (1958): "environmental interpretation is the ultimate aim of facies studies, but environment is not facies. It

produces facies." An environment is a geographical unit with a particular set of physical, chemical and biological variables (Reading 1978).

In practice, lateral variations in marine depositional environments often result in a vertical succession of facies as the shoreline moves landward (transgression of sea or erosion of land) or seaward (regression of sea or progradation of land: e.g. Walther's Law, 1894, see Blatt et al. 1972). A facies model can be derived from studies of ancient rocks and recent environments and is a general summary of a specific sedimentary environment (Walker 1979). A facies model can be used to predict the vertical succession of strata that would result from lateral migration of adjacent environments. It can also be used as a framework for investigating other sedimentary rocks presumed to have been deposited in this specific environment. The model can then be tested with the observed succession of objectively defined facies in a subsequent investigation. Detailed descriptions of recent sedimentary environments are a vital link in this scheme.

In the next section I describe the regional environment of deposition around Tentsmuir Beach and successively narrow my focus to consider: the beach (a depositional environment), the study area (a sub-environment of deposition) and field divisions of the study area. This detailed description of the environment is then related to objective aspects useful for sedimentological and ecological analysis. In this way, a rather detailed investigation of an areally restricted and geologically transient phenomenon can be made accessible to parallel investigations of coastal landforms, processes and faunal communities and speculations on the nature of depositional environments based on facies analysis.

2.1.1 Regional environment.

Tentsmuir Beach is situated on the north east coast of Fife, Scotland between the mouth of the River Tay and the mouth of the River Eden (Figure 2-1). The beach is a straight 7 km stretch of the western margin of St Andrews Bay and is associated with the extensive intertidal deposit, the Abertay Sands.

Recent work on the sedimentology of this region includes studies of the Tay and its southern entrance (Green 1974,1975, Buller 1975, Buller and McManus 1975, Buller et al. 1975, McManus et al. 1980); a study of the Eden (Eastwood 1977) and a study of nearshore processes in St Andrews Bay (Ferentinos and McManus, in press). Chisholm (1971) and Cullingford (1972) detailed the post-glacial shoreline development. Khayrallah and Jones (1975) surveyed the benthic fauna of the Tay and Green (1975) investigated the distribution of macrofauna at the southern entrance.

The bar at the mouth of the Tay has a mean tidal range at spring tides of 4.7 m and at neap tides of 2.3 m (Admiralty Tide Tables). This can be classified as a mesotidal environment (Davies 1964) and the Abertay Sands as a shoal or marginal linear sand bar associated with the ebb-delta (Oertel and Howard 1972, Hayes 1975 and Ferentinos and McManus in press). Secondary flood channels, swash bars and swash platforms are developed on the Abertay Sands (Oertel 1972, and Figure 2-2).

The Tay is a partially mixed estuary with pronounced tidal flushing at the entrance, which transfers suspended material and pollutants from the outer estuary to the sea (Williams and West 1975, Charlton 1980). The supply of suspended sediment to the outer estuary is intermittent, dependent on wind fetch and velocity and tidal state and amplitude. The primary source of suspended sediment is resuspension of tidal flat material through the interaction of tidal currents and wind-induced waves (Buller 1975).

Tentsmuir Beach is a raised-beach platform covered with about 18 m of Recent (13,000-6,000 yrs.B.P.) and post-glacial deposits (Green, 1974 and Chisholm 1971). The present beach and nearshore sands have developed in response to tidal currents and wave induced longshore currents (Ferentinos and McManus, in press). St Andrews Bay has a gently sloping bottom topography (Figure 2-1) and is subject to considerable wave action. Wind generated wave action is most significant from the southeast and northeast as westerly winds are short-fetched. Ferentinos and McManus (in press) predicted that northeast and southeast winds generate northwards flowing longshore currents along Tentsmuir Beach and westward currents along the seaward margin of the Abertay Sands. Tidal water movement is parallel to Tentsmuir Beach, controlled by the channel geometry between the shore and Abertay Sands. Flood waters flow along Tentsmuir and turn westwards when entering the main channel of the Tay (Green 1975 and Figure 2-2). Ebb waters drain the tidal flats at Tayport and flow southeastwards over the Abertay Sands into St Andrews Bay. As the waters drain off the intertidal shoal, the nearshore flow is directed into the secondary channel and southwards along Tentsmuir Beach (Figures 2-2).

Green (1974) has demonstrated a clockwise sediment transport gyre around Abertay Sands. Ferentinos and McManus (in press) suggested that sediment brought northwards by the longshore current and eastwards by the River Tay may be trapped by this gyre and deposited on the banks of the channel.

The foreshore of the beach is dominated by ridge and runnel topography, the troughs of the secondary channels by current ripples and the backshore by foredunes parallel to the shore. Analyses of the migration of H.W.M.O.S.T. and L.W.M.O.S.T. have demonstrated that the northern part of Tentsmuir is an area of rapid progradation due to accretion of sand in the gyre and landward transport of dried sands during onshore winds (Green 1974, McManus et al. 1980, Ferentinos and McManus in press). Dunes are rapidly stabilised into ridges with intervening areas of dune slacks (Crawford 1965).

The surface sediments of Tentsmuir Beach, Abertay Sands and St Andrews Bay are mainly composed of well sorted, fine to very fine sand (McIntyre 1958, Green 1974, 1975, McManus et al. 1980, Ferentinos and McManus, in press, and Chapter 4). The source of recent sediment supply is unknown. Cullingford (1972) suggested erosion of post-glacial raised beach deposits as a source, Ferentinos and McManus (in press) however considered this supply inadequate and proposed reworking of unconsolidated sediments on the floor of St Andrews Bay. Whatever the source, the sediment throughout the area is exposed to strong wave and current forces and is very homogeneous. Deposition of suspended sediment is negligible, the supply from the estuary is apparently well dispersed by the flushing and

circulation of the outer estuary and most suspended sediment is carried through the channels without settling (Buller 1975, Charlton 1980).

Currents within the Tentsmuir channel have been measured in excess of 1m s^{-1} (Green 1977, Ferentinos unpublished data). Two sections of the channel experience the strongest current velocities and exhibit ebb dominated megaripple trains: the Pool, located at the northernmost section of the channel; and the area considered by this study, located at the southern end of the channel (Figure 2-2). Between these areas the channel widens and subdivides producing wide, flat bars.

The geometry of the Abertay Sands is controlled by two major conflicting forces, the northward longshore drift of sediment meeting the seaward ebb of water and suspended sediment from the Tay. This produces a roughly triangular area of sand, modified by flood and ebb streams flowing along Tentsmuir Beach. The result is a dynamic sand body with a western channel sheltered from wave trains generated by the northeast and southeast waves. The tidal current within this channel is slack for less than four hours within a 24 hour cycle (pers. obs.). The upper shore of Tentsmuir Beach is extensively reworked by wave movement and is very unstable (Green, 1974 and pers. obs.). However the lower foreshore within the shelter of the Abertay Sands is only subjected to strong wave disturbance when the onshore swell combines with tides higher than mean tide level.

2.1.2 Study site

The site chosen for extensive observation was located entirely below mean low water neap tides and within the area of foreshore protected by the swash bar of the Abertay Sands. Its approximate boundary was determined by the distribution of aggregations of Lanice tubes in October 1977. The 15,000 m^2 area consisted of a "low tide platform" (between low water neap and low water spring tide levels) bounded by a gently sloping beach (less than 10° slope from high water spring to low water neap) to the west and a steeply shelving channel margin ($20-30^{\circ}$) to the east. A sand bar formed by migrating megaripples formed a shallow embayment at low water (Figure 2-3). The secondary tidal channel narrowed at this point and the tip of the flood ramp separated two ebb channels, which joined just south of the study site (Figure 2-2). The swash bar formed the seaward margin of the secondary tidal channel with a steep lee slope.

The study site changed markedly in appearance from summer to winter as bedforms stabilized or migrated, algal species came and went and strong easterly swells disturbed the channel geometry. The general description above remained remarkably stable until November, 1980 when the embayment filled with sand and the megaripple field moved southwards 200 m. This abrupt, though relatively small, change was attributed to alterations in channel geometry and distribution of flow regimes and is very common in intertidal sand bodies such as the Abertay Sands (Oertel and Howard, 1972, Robinson 1975). The distribution of Lanice was also subject to small-scale changes, but local fishermen confirm that aggregations of Lanice and associated sedimentological features described below have been present on a

1000 m stretch of Tentsmuir Beach for over 15 years (Wm. Ireland, pers. comm.).

Tentsmuir Beach was subject to semi-diurnal tides with most spring tides falling in the early morning and early evening. The nature of the study area (flat platform, bounded by sloping margins) and the large tidal range (4.7 m spring tides) resulted in very rapid flooding and draining. This restricted field observations, particularly in situ experiments (e.g. resin peels of internal structures in trenches).

The substratum in the study area consisted of well sorted fine sand mixed with shell debris (see Section 4.1) and exhibited a variety of bedforms developed in response to moderate bidirectional currents. With the exception of the periods of exposure, the study area experienced almost continuous current activity as slack tides usually consisted of oscillations between flood and ebb currents followed by a strong reversal of flow, while most wave activity was confined to the sloping beach. Apart from two observations at high tide with SCUBA equipment, the area was studied at extreme low water spring tides and consequently the surface features and sediment characteristics described below reflect the effects of ebb tidal currents.

2.2 Methods

2.2.1 Grid system and transect.

The difficulty of access and rather featureless nature of the beach necessitated a robust system of marking positions within the study area, rather than resurveying each sampling point and observation. After an initial period of reconnaisance, the study area was defined, a grid established and markers placed as needs arose. The base line of the grid was chosen sub-parallel to the shoreline and dominant current direction. The grid was surveyed to a levelled post in the dune area behind the beach and two prominent observation towers marked on charts (Figure 2-2).

Positions were marked with 1.5 m lengths of 2 cm steel conduit, hammered 1.4 m into the beach. These marker poles were suitable for two field seasons, less robust markers were quickly fouled by algal debris and swept out by the current.

The base line was marked with twelve poles, 10 m apart placed along a bearing of 027° (magnetic). Most observations were referred to this line or temporary grids established at each tide. The base line is numbered 1-12 (south to north) on Figure 2-3.

A transect line was chosen to include as many variations in apparent worm density and sedimentological environments across the study area as possible. This line consisted of 9 poles, 10 m apart established on a bearing of 098° (magnetic) from pole 7 of the initial grid. The transect served as a sampling line and each pole (including pole 7) was designated by a station number (1-10).

A third line extending eastwards from pole 12 was marked parallel to the transect line. This line consisted of 3 poles, 10 m apart and is labelled A-D on Figure 2-3. These positions were established to permit field experimentation without disturbing the sampling stations.

Three further poles were placed along the eastern boundary of dense Lanice settlement between the transect line and experimental station 'D' (Figure 2-3). The poles were placed at this position in September, 1978 to permit comparison with settlement distribution in 1979.

2.2.2 Beach profiles.

The profile was surveyed from the levelled post in the dune area. It was measured along a bearing of 115° (magnetic) from this post to pole seven established in the grid base line (Figures 2-2, 2-3). The profile was extended (23.4.78, 9.5.78, 21.5.78) into the research area along a bearing of 95° (magnetic) from this pole. On these three occasions very low tides allowed a complete profile to be surveyed. The extended profile

roughly corresponds to the transect line.

Profiles were measured by a method derived from Stephen (1977) which allows rapid measurement by one person. The profile was surveyed at monthly intervals between February, 1978 and March,1979 apart from June, July, November and December when tide conditions did not permit a full survey (Figure 2-4).

2.2.3 Observations

The observations of and sample collecting in the study area were selected to elucidate two interacting processes, the sedimentological regime and the infaunal community structure. On the basis of surface observations at low spring tides eight field divisions were distinguished to facilitate comparison of observations with laboratory analyses of samples. Each station on the transect was assigned a field division for each collecting period and laboratory analyses of sediment structure, grain-size characteristics, and infaunal distribution and abundance were later related to each division. This approach provided the framework for the following three chapters. Surface features observed at Tentsmuir Beach are described and the field divisions are outlined, including their distribution on the transect at each sampling time (Chapter 3). The grain-size characteristics and sedimentary structure (physical and are then detailed, where available for each field division (Chapter 4). The abundance of infaunal species in each division and effects of predation and larval settlement for the study area are described in Chapter 5.

Figure 2-1

Location of Tentsmuir beach.

Depth contour lines from Admiralty Charts (1978). L.W.O.S.T.: Low water ordinary Spring tide. E.L.W.S.T.: Extreme low water Spring tide. 10 m: 10 m below Ordinance Datum (O.D.). 20 m: 20 m below O.D. Rectangle indicates location of area in Figure 2-2.

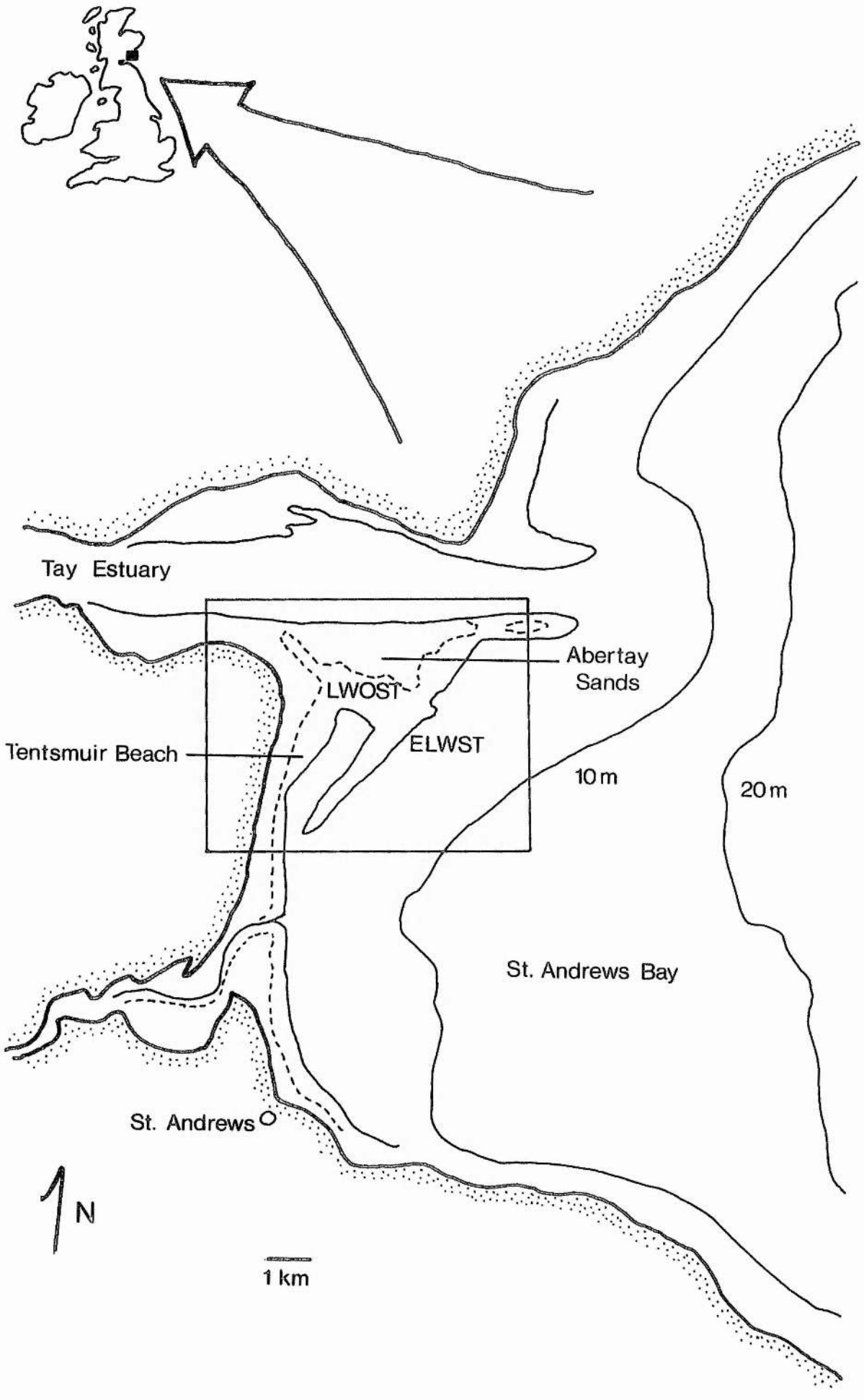

Tay Estuary
Abertay
Sands
LWOST
ELWST
Tentsmuir Beach
10 m
20 m
St. Andrews Bay
St. Andrews
N
1 km

Figure 2-2

Current and wave patterns in vicinity of Tentsmuir beach and location of study area. Derived from Green (1977), personal observations, Admiralty charts (1978) and aerial photographs (1978).

a. Current and wave patterns in the vicinity of Tentsmuir Beach. Derived from Green (1977), personal observation and Admiralty charts (1978). Rectangle indicates location of Figure 2-2b. Ebb current flow distribution indicated by open triangles and flood current flow direction by solid triangles. Dominant wave directions indicated by open arrows.

b. Location of study area at Tentsmuir Beach.
Traced from an aerial photograph taken by Fairey Aerial Surveys in August 1978. The areas occupied by dense aggregations of Lanice conchilega and algae were visible on the photograph and are indicated by hatching.

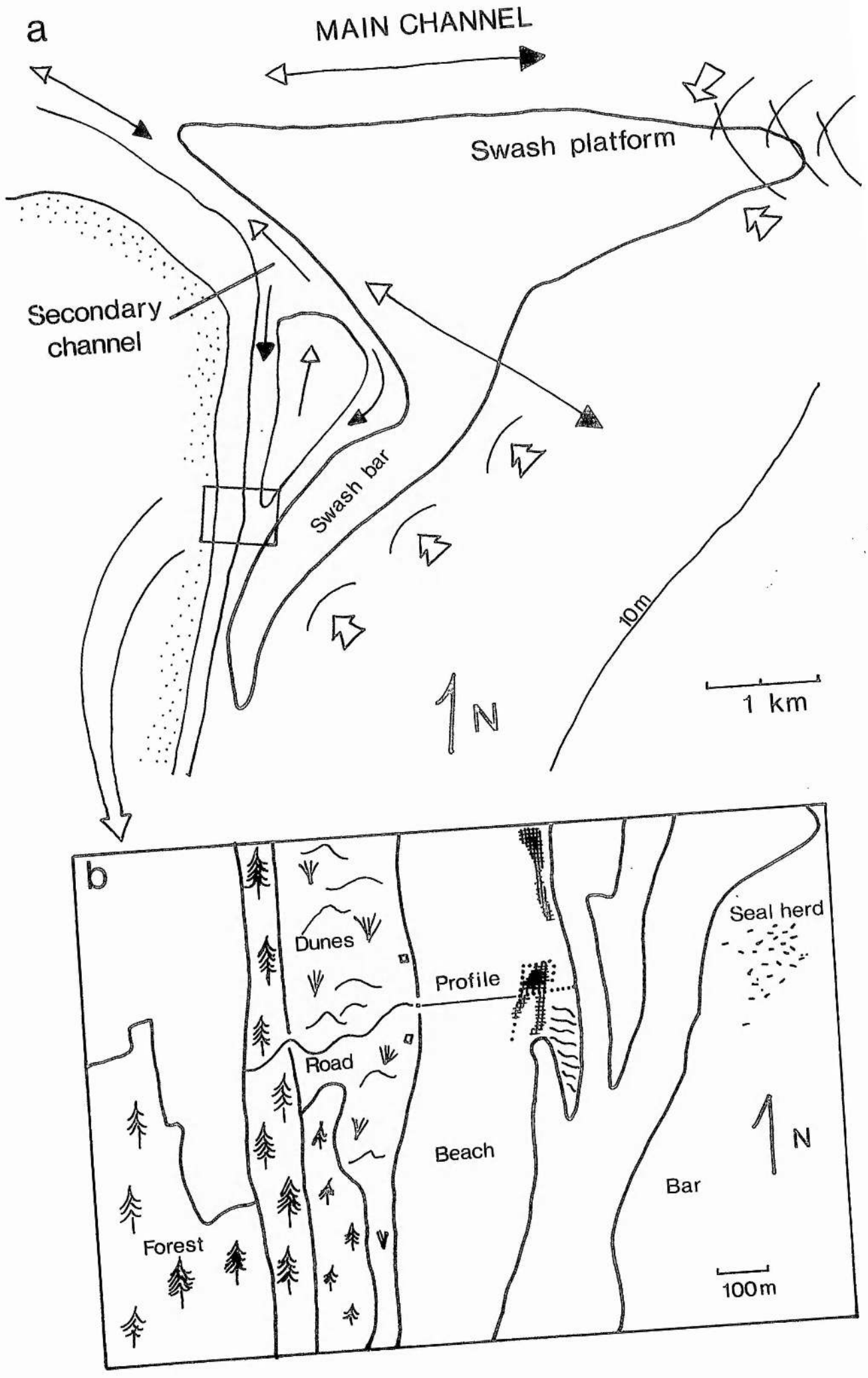

a
MAIN CHANNEL
Swash platform
Secondary channel
Swash bar
10m
N
1 km
b
Dunes
Profile
Seal herd
Road
Beach
Bar
Forest
N
100m

Figure 2-3

Diagram of study area at Tentsmuir beach showing: physiographic features, tide marks, grid system and transect.

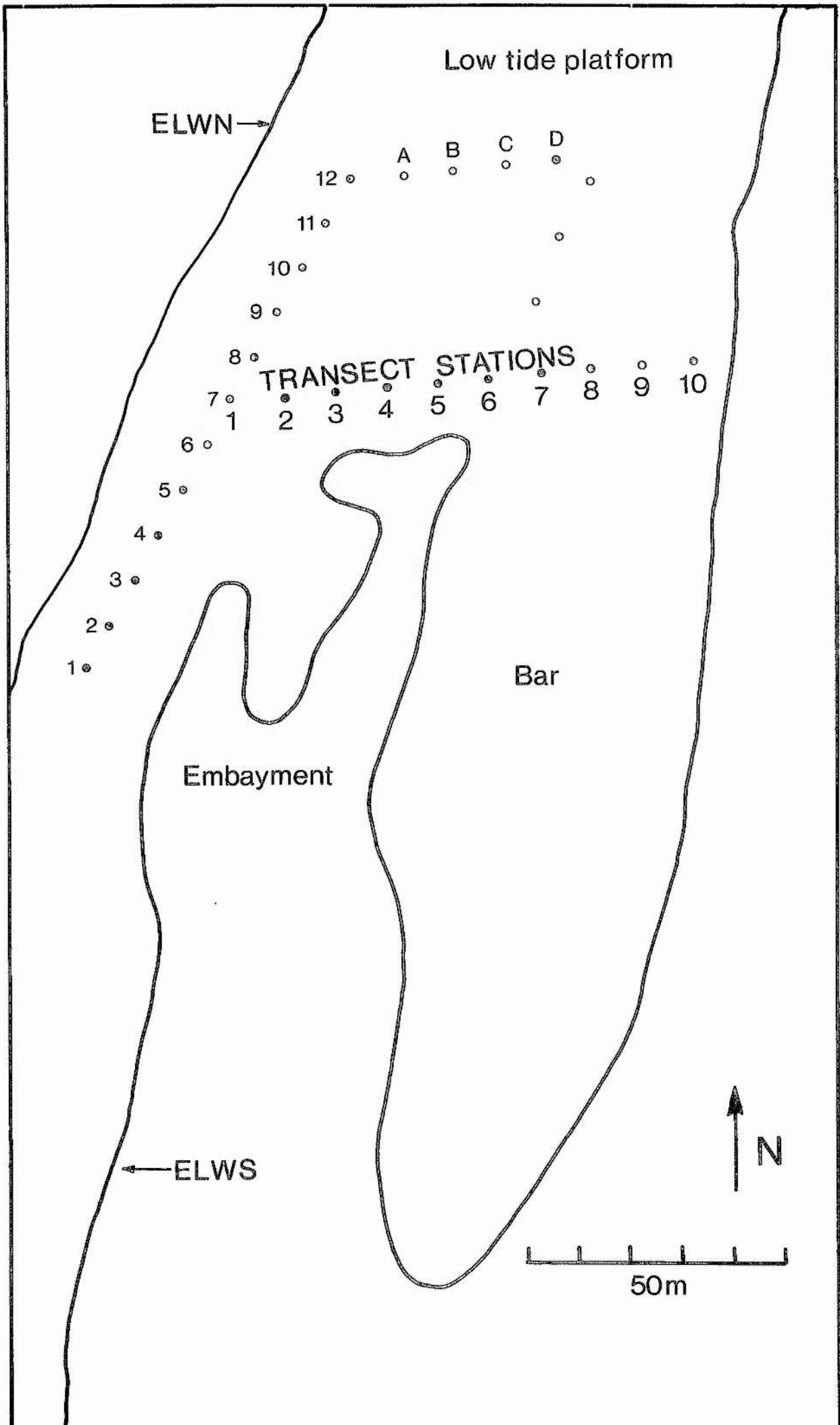
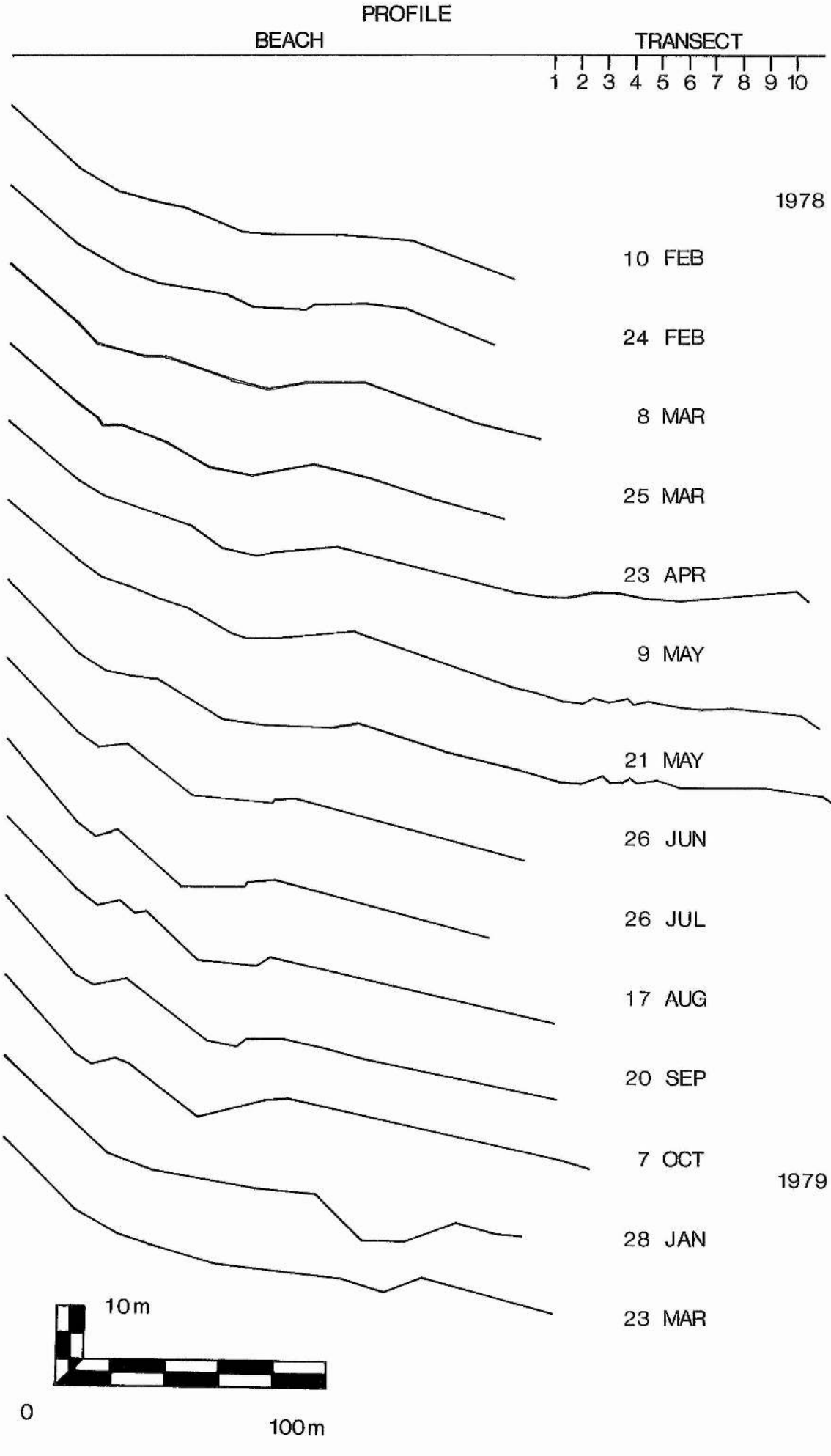

Low tide platform
ELWN
A
B
C
D
12
11
10
9
8
7
6
5
4
3
2
1
TRANSECT STATIONS
1 2 3 4 5 6 7 8 9 10
Bar
Embayment
ELWS
N
50m

Figure 2-4

Beach profiles measured along line on Figure 2-2b, from a reference post in the dunes to the transect and along the transect (23 April 1978, 9 May 1978, and 21 May 1978) to the edge of the tidal channel (extreme low water spring tide level). The first three profiles represent a storm or 'winter' profile with a characteristic low angle beach slope and on this beach a fairly smooth profile. From the 25 March 1978 profile the swell or 'summer' profile begins to develop with a characteristic high angle beach slope and a notched profile indicating the development of a ridge and runnel topography. This profile shape was flattened slightly by spring storms before the 23 April profile but the swell profile is well-developed by 26 June 1978. Storms began to modify the profile before 20 September 1978, reducing the seaward ridge and continued to do so throughout October. Severe winter storms combined with spring tides in late December and early January altered the beach profile extensively. This modification combined with runnel migration along the shore displaced the runnel 70m toward the sea by 28 January 1979.

Note the development of algal-Lanice mounds along the transect between 23 April and 21 May.


PROFILE
BEACH
TRANSECT
1 2 3 4 5 6 7 8 9 10
1978
10 FEB
24 FEB
8 MAR
25 MAR
23 APR
9 MAY
21 MAY
26 JUN
26 JUL
17 AUG
20 SEP
7 OCT
1979
28 JAN
23 MAR
10m
0
100m

3 Chapter 3 *Lanice* tidal channel sub-environment

3.1 Description of sub-environment

The *Lanice* tidal channel sub-environment developed in linear patches along a secondary tidal channel associated with an ebb-delta shoal environment. It was distinguished from other areas of the channel and beach-shoal complex by the presence of dense (>100 individuals m^{-2}) aggregations of the tube-building polychaete, *Lanice conchilega* (Pallas 1766). *Lanice* constructed vertical tubes of sand grains and shell fragments which projected 1-5 cm above the sediment surface. Distinctive surface features were developed around these tubes and some features were related to emergence (late stage run-off and predation).

The sub-environment was restricted to a zone between neap low water and a few metres (channel depth) below spring low water. The features associated with emergence were restricted to a zone below neap low water and above extreme spring low water.

The distribution of the patches along the tidal channel was irregular. The patches developed within the channel and along low-tide platforms at the margins of the channel, and were a persistent feature of the channel. Eroded patches were re-colonised by sub-tidal larval production and/or production within the sub-environment.

The patches did not extend up the shoreface but did extend sub-tidally with a maximum width equivalent to the width of the tidal channel (300 m). Most patches were observed to be 10 - 50 m wide and 100 -200 m long, parallel to the channel axis.

The intertidal exposure of a Lanice tidal channel sub-environment revealed a surface dominated by current bedforms and an irregular topography of mounds, ridges, tidal pools and drainage channels (Figure 3-1a). The patches were a focus for the feeding efforts of birds and flatfish and numerous distinctive feeding traces have been observed. The margin of some patches was marked by an abrupt lateral change in the distribution of Lanice (Figure 3-1b).

3.2 Surface features and bedforms.

Field observations included mapping of bedforms and description of sedimentological features associated with Lanice tube-building activity. Distribution of bedforms and features is discussed in Sections 3.3 and 3.4.

Description of bedforms and quantitative indices generally followed Reineck and Singh (1975), however some features encountered were clearly generated by Lanice and derivative terms were developed. An attempt has been made to combine features of Allen's (1968) and Reineck and Singh's (1975) terminology. Allen provided a comprehensive system for describing

current ripples but this system was overly complex for the needs of this study. His approach has been used in the description of some features associated with ripples (ripple fans, spurs). Reineck and Singh simplified Allen's system and extended their coverage to biogenic features, and surface features other than current ripples (Figure 3-2). They unnecessarily modified a few terms (lingoid for linguoid, length for chord) and these have been retained as in Allen (1968).

3.2.1 Current Ripples

Reineck and Singh (1975) differentiated four major types of current ripples. Two of these major types were recognized at Tentsmuir: small ripples and megaripples.

Small ripples are asymmetrical undulations on a bed surface produced by current. They range in chord between 4 and 60 cm and the height varies between 0.3 and 6 cm (Figure 3-2). Ripple index (ratio of chord to height, Bucher, 1919) is greater than 5, generally 8-15. Reineck and Singh (1975) described a transition series of three types of small ripples: straight-crested, undulatory and linguoid. These represent stages in a continuous velocity series, straight-crested representing the low velocity endpoint and linguoid the high velocity endpoint. Reineck and Singh (1975) and Allen (1968) suggested that there is a tendency for the crests of ripples to become discontinuous or lobate with an increase in the energy of the environment, due to increase in velocity or decrease in water depth. This supposition was accepted in this study and their terminology provided

a simple, clear framework to describe the sedimentological environment at Tentsmuir.

Another type of small ripple occurred at Tentsmuir, described as rhomboid by Reineck and Singh (1975). These develop when a very thin layer of water washes over a bed at high velocity and are generally associated with backwash on beaches.

Megaripples are defined as ripples that exceed 60 cm in chord and 6 cm in height; their ripple index is between 10 and 100 (Reineck and Singh, 1975 and Allen, 1968). Megaripples can be arranged in a transition series: straight-crested, undulatory and lunate. The undulatory stage combines Allen's (1968) catenary and sinuous megaripples. This transition series represents increasing velocity or decreasing depth.

3.2.2 Features associated with current ripples

A number of features have been described that appear in the troughs, lee- or stoss-sides of ripples. Four of these features have been recognized at Tentsmuir: spurs, ripple fans, rill marks and water level marks.

Spurs are raised ridges, parallel to the flow, that arise from the lower slipface or upper bottomset of one ripple and extend over the stoss side of the next. Between spurs laterally, are broad furrows with rounded floors (Allen, 1968). Spurs and furrows are most notable in association

with undulatory megaripples, where they appear as deep scour pits.

Ripple fans are patterned assemblages of small ripples that occur in the furrows between spurs and up the stoss side of megaripples (Allen, 1968).

Rill marks are bifurcating, dendritic erosional sculptures made by a system of small rivulets (Reineck and Singh, 1975). They are formed under a flow of less than 2 cm depth on a sediment surface during the process of sinking water level (Cepek and Reineck, 1970). Rill marks are a criterion for intermittent subaerial exposure.

Water level marks are horizontal ridges formed on the slopes of emerging bedforms due to discontinuously falling water level (Häntzschel, 1939).

3.2.3 Obstacle marks

Obstacle marks are formed by stationary obstacles deflecting the flow lines of currents and creating erosion, deposition or both behind the obstacles (Reineck and Singh, 1975). Current crescents are obstacle marks that consist of a small ridge tapering downcurrent behind an obstacle and a semicircular depression on the upcurrent side of the obstacle (Sengupta, 1966). These were commonly formed at Tentsmuir around projecting Lanice tubes and biogenic volcanoes.

3.2.4 Algal flow lineations, mounds and islets

Two important sedimentological consequences of algal growth in the sediment are: flow lineations and mound building.

Flow lineations are produced when attached algal thalli are gently lowered to the surface by the receding tide. Eastwood (1977) described a technique of assessing flow direction just prior to exposure utilizing the orientation of attached algal strands in the Eden Estuary. The orientation of the thalli provides a clear indication of flow directions in the late stages of ebb tide. His identification of the strands as Chaetomorpha sp. was probably mistaken (Zenetos 1980, per.obs. 1978), however his observations are of considerable value.

At Tentsmuir various algal species appeared in the summer. Of importance to sedimentological investigations are species of the genera Enteromorpha and Polysiphonia. The thalli of these species can grow as long as 60 cm and are attached to small shells, worm tubes and pebbles buried in the sediment. These algae are capable of growing up through deposited sand layers and stabilizing the substrate. They do not form a true algal mat and the tubular thalli are not capable of binding sediment, but their rapid growth and extensive replication produces a dense thicket which slows sediment transport and is resistant to erosion. A recent study by de Boer (1981) showed that micro-organisms (such as blue-green algae, diatoms and bacteria) are also capable of stabilizing megaripples.

Mounds were produced at Tentsmuir through the association of Lanice tubes and attached or adjacent algal thalli. Observations indicated that aggregations of tubes or clumps of algae on their own do not result in mounds larger than a few centimeters.

Mounds observed at Tentsmuir appeared to conform to similar physical constraints to megaripples. Although they did not migrate themselves, small ripples migrated over the mounds and growth was pronounced during maximum spring tide cycles. Orientation was normal to current flow and most mounds assumed an elongated undulatory form. Maximum height was 45 cm with most mounds reaching 20-30 cm. Maximum chord was 2 m, but most mounds were much less than this. Mounds had flat to rounded crests and steep sides, often symmetrical in profile. Internally, mounds were generally composed of dense layers of horizontal algal thalli, shells, sediment and tube tops interspersed with thick layers of sediment penetrated by vertical tubes without tops and vertical thalli (Chapter 4).

Macro- and microalgae are common intertidal organisms, and extensive growth of algae in summer is known to result in sediment accretion (Hommeril and Rioult 1965, Frostick and McCave, 1979). The localized source of attachment provided by aggregations of Lanice tubes increased the likelihood of successful settlement and growth and created discrete areas of accretion. In turn, the stabilization and accretion associated with the growth of algal thalli appeared to enhance the settlement of juvenile Lanice. The observed increase in settlement of Lanice may have been due to chemical factors or (more likely) purely hydromechanical factors. The result, however, was increased attachment sites for algal sporlings. As

sediment accumulated, algae and worms maintained contact with the sediment surface by extending thalli and tubes vertically.

Allen and Friend (1976) and Nio, et al. (1980) reported an increase in threshold velocity for bedform migration after neap tide cycles. De Boer (1981) suggested that this observed increase in theshold velocity may have been the result of a gradual increment of the surface organic layer during the standstill of migration at neap tide.

After algal thalli died in October and Lanice slowed its tube building activity, substantial erosion of algal-Lanice mounds occurred. Winter storms and high tides produced strongly erosive conditions; after sections of mounds and flats were removed, the remaining clumps were further modified by currents and longshore sediment transport. This resulted in flat-topped mounds which stood out in relief from the surrounding sediment. Erosional remnants such as this have been described by Macar and Ek (1965) from the Devonian of Belgium and by Klein (1977) from the Minas Basin, Bay of Fundy. These islets (or ilôts) may have fan-shaped current ripples associated with them as the mound deflects currents in shallow water around the perimeter. I have observed islets at Tentsmuir with fan-shaped ripples and also prisms of sand that migrated from one side of the islets in ebb flow to the opposite side during flood. As one side is exposed, tube tops and biogenic volcanoes are revealed and a rather complex morphology results (see below Figure 3-11).

3.2.5 Lebensspurren.

Some surface sedimentary features recognized at Tentsmuir have been classified as recent lebensspurren; comparable structures have been recognised in the fossil record (fossil lebensspurren). Lebensspurren were defined by Reineck and Singh (1975) as sedimentary features formed as a result of animal activity that are large enough to be recognized.

3.2.5.1 Biogenic volcanoes.

Sediment volcanoes are associated with expulsion of sediment-laden water as a result of slumping, very rapid sedimentation or agitation of freshly deposited sediment (Reineck and Singh, 1975; Gill and Kuenen, 1958). Biogenic volcanoes are small (less than 5 cm in any direction) surface features formed by tube or burrow-dwelling organisms in response to rapid burial and exhumation. Biogenic volcanoes are thus biologically induced sediment volcanoes associated with small animal dwellings and rapid sediment influx. Volcanoes formed by Lanice were characterized by a dome formed of mucus-stiffened sediment surrounding the top of the erect tube or burrow (Figure 3-3a). The size of the dome was determined by the size of the tube or burrow and the level of exhumation, as a general guide the diameter of the base of the dome rarely exceeded five times the diameter of the tube. The opening to the tube or burrow was depressed within the rim of the dome.

The biogenic sand volcanoes produced by Lanice were formed by expulsion of sediment, water and mucus in a jet after rapid sedimentation. Sedimentation usually resulted from periodic migration of bedforms across isolated Lanice mounds (Figures 3-3a and 3-11). Tube tops were rapidly buried with a thin (1-5 cm) layer of fine sand, and on reversal of the tide (or further movement of the bedform) rapidly exhumed. This process left the tube full of fine sand and projecting 1-3 cm above the surface. The animal responded by ejecting a mixture of sediment, water and mucus, with sufficient force to regain contact with the surface. Propulsion was accomplished by rapid peristaltic movements of the animal in its tube. The ejected material fell around the tube and retained a stiff consistency from the mucus content. If the tube was not exhumed the worm burrowed to the surface. If the tube was exhumed to such an extent (greater than 4-5 cm) that the tube collapsed, the worm escaped from the side of the base of the tube. In either case the burrow wall was lined with mucus to form tube walls and sediment was expelled at the surface and formed a biogenic volcano.

Biogenic volcanoes were not recognizable as either of Reineck's (1958) types of burrow coating. He interpreted both types as material added to the interior of the burrow. Arenicolids expel sediment during normal feeding activity but this is not comparable to tube clearing actions. Arenicola swallows slumped sediment and expels characteristic coiled faecal masses (see Fauchald and Jumars, 1979 for review), it does not maintain a rigid burrow or tube wall. Reineck and Singh (1975) reported that Corophium "blows" out unwanted sediment, but they did not comment on any structures formed by this activity. Biogenic volcanoes may be formed at

the end of escape structures or around established tube or burrow openings. The structures are not expected to occur extensively as preserved internal features as they are associated with reworking and bioturbation. Biogenic volcanoes may be preserved as surface features under exceptional conditions, sudden burial of sand flats with fine-grained sediments might produce casts or moulds.

Hill and Hunter (1976) reported 'chimney structures' formed around the openings of Callianassa islagrande (ghost shrimp) burrows on Padre Island, Texas. These structures were attributed to erosion of the burrow opening and are remarkably similar in appearance and size to the biogenic volcanoes formed by Lanice (compare their Figure 19B to Figure 3-3a). In both cases the size of the chimney or volcano is 2-3 times greater than the normal diameter of the tube (Hill and Hunter reported C. islagrande burrows to be 6-7 mm in diameter near the surface; the chimneys figured are about 2 cm in diameter). Hill and Hunter (1976) found that C. islagrande disposed of some excavated sand by venting it out of the burrow opening. Thus, it is very possible that both structures were formed by comparable processes. Both organisms construct deep vertical burrows in the nearshore zone and these structures were formed by reworking of surface sediments by waves and currents in protected bar-trough or bar-tidal channel environments. A preserved burrow opening of this kind should be indicative of a shallow water environment protected from storm wave activity.

Fossil lebensspurren of comparable scale and shape have been described from the lower Carboniferous (Donaldson and Simpson 1962), upper Cretaceous (Chamberlain 1971b) and upper Devonian (Gutshick and Rodriguez 1977). They were described by Donaldson and Simpson (1962) as Chomatichnus wegberensis:

small circular mounds consisting of fecal castings, about 5-7 cm high, connected with a vertical burrow (see also Häntzschel 1975, 1939). Simpson (1970) has attributed these structures to castings produced by the Zoophycos animal, based on their co-occurrence at the original locality. Subsequently they have been found associated with Ophiomorpha and Thalassinoides burrows which are attributed to shrimps (Chamberlain 1971b, Gutshick and Rodriguez 1977). In one context Chamberlain (1971b) stated: "C. wegberensis in northwestern New Mexico was probably preserved in a lagoon subjected to tidal current scouring but protected from direct wave agitation and pounding". It is most commonly found in sandstones overlain by shales (Gutschick and Rodriguez 1977).

3.2.5.2 Eider browsing traces.

Lebensspurren formed as a result of organisms feeding on a sediment surface are termed browsing traces (Seilacher, 1953). Numerous, small browsing traces were found at Tentsmuir (bird footprints, beak marks) that have been described elsewhere (Schäfer, 1972). One type of browsing trace was very important sedimentologically and ecologically at Tentsmuir. This trace was formed by browsing eider ducks (Somateria mollissima). The ecological consequences of eider browsing are discussed in Chapter 5. The sedimentological effects are discussed here.

Eider -browsing produced a shallow circular depression up to 50 cm in diameter and 15 cm deep. Most depressions filled in quickly as wet sediment slumped from the sides. These shallow depressions in mobile sand were eradicated by rising tide and only rarely persisted until the following ebb tide. Some traces occurred in firm sand buttressed by high densities of Lanice tubes (Figure 3-3b). These depressions did not fill quickly and remained as conspicuous holes maintained by the tidal currents.

Both types of eider browsing traces caused disruption of pre-existing internal sedimentary structures and provided sites for erosion by tidal currents. Although Tentsmuir was not regarded as an environment with high preservation potential, these traces occur in other intertidal environments (Player 1971). The traces formed as eiders excavated in the soft sand for recently settled bivalve spat (see Chapter 5). Eider traces may be expected to occur near extensive mussel beds, as these bivalves are their primary source of food (Pethon 1967, Dunthorn 1971, Pounder 1971).

Eider browsing traces can produce circular scour pits 20 to 50 cm in diameter, associated with severe, local disruption of bedding structures to a depth of 15 cm. There is evidence that ripple fans in megaripple furrows have been fossilized (Pettijohn and Potter, 1964 and Allen, 1968). Eider browsing traces are of a comparable scale and structure and occur in soft, fine sediment in shallow coastal environments.

A comparable feeding trace has been described from modern intertidal sediments, Pleistocene sands, and upper Cretaceous sandstones (Howard et al. 1977). This trace was attributed to the feeding activity of rays (elasmobranchs) on tidal flats, estuarine sand bars and tidal channels. The rays produced structures 6 cm - 1 m in diameter with a shallow, dish-shaped depression 6 cm deep and a roughly circular hole up to 30 cm deep. The deep hole was filled by current bedload as soon as the ray stopped feeding, but the walls did not collapse. The shallow part of the structure filled more slowly, with concave upwards laminae of sand and mud.

Interestingly, the recent ray feeding traces occurred in fine sand with abundant tube-building polychaetes (Onuphis microcephala and Diopatra cuprea; both of similar size to Lanice) and deep-burrowing shrimps (Upogebia affinis, Callianassa major, and C. atlantica) which form an important part of the diet of some ray species (Dasyatis sabina, D. sayi, D. americana). The preserved traces have been found in fine sands with the fossil lebensspurren Ophiomorpha and in one case (Pleistocene, Florida-Georgia State Line) also with numerous polychaete burrows and dwelling tubes. All of the fossil lebensspurren reported by Howard et al. (1977) occurred in strata interpreted as shallow coastal environments.

Risk and Craig (1977) reported flatfish feeding traces from the Minas Basin, Bay of Fundy and attributed them to flounders (Liopsetta putnami or Pseudopleuronectes americanus). Similar species of flatfish (Pseudopleuronectes platessa and Limanda limanda) were common as juveniles

in the Lanice area, especially in intertidal pools. The traces from the Minas Basin were small (3-5 cm deep and 2-3 cm in diameter) and occurred on muddy tidal flats. No traces of this kind were observed at Tentsmuir, but the flatfish were presumed to have an important effect in maintaining low tube densities in the pools (see Chapter 5) and therefore an important effect on the sediment structure in the algal-Lanice association.

3.2.6 Divisions of Lanice tidal channel sub-environment

The Lanice tidal channel sub-environment, although limited in area (study area = 15,000 m^2) exhibited a complex pattern of bedforms and organic structures (ripples, channels, banks, tubes, algal thalli) through time. To facilitate description of the exposed surface, field characteristics were grouped into eight units. Each unit represented a division of the sub-environment; some of these units were not restricted to this particular sub-environment. The presence of three or more units was only observed within the Lanice tidal channel sub-environment. Preliminary observations (October 1977 to February 1978) provided field data for the initial grouping; the divisions recognised at this time were expanded in May 1978 when settlement of L. conchilega and algae produced new surface features. Divisions recognised in May 1978 proved to be robust enough to remain unchanged throughout the study despite the addition of new field data.

The divisions were discriminated on the basis of surface features present (bedforms), densities of projecting tubes and topography. The distributions of the divisions at any point in time were non-overlapping, therefore maps of divisions were compiled and related to samples collected on a grid. This allowed comparison of surface features with internal features (macroinfauna, grain size, sedimentary structures).

In Chapter 4, internal structures and grain-size characteristics are described and related to each division. In Chapter 5, ecological features of macrofaunal species are described and related to the field divisions. The distribution of the divisions in August, 1978 and January, 1979 is shown in Figure 3-5 and Figure 3-6 respectively. Figure 3-5 can be compared with a view looking east across the study area in September 1978, Figure 3-4).

The surface features were controlled by large-scale physical factors (waves and currents) and small-scale biological factors (polychaete tubes, algal thalli). The Lanice tidal channel sub-environment was characterised by the presence of Lanice tubes, intermittent sub-aerial exposure, protection from wave action, exposure to moderate bidirectional currents, and location within an intertidal sand complex associated with a mesotidal estuary. Each field division exhibited unique characteristics which were related to one or all of the characteristics common to the sub-environment. The characteristics and surface features of each field division are summarized in Table 3-1. The eight field divisions are described below.

3.2.6.1 Beach face.

The beach face division was recognised by the attitude of the surface to the horizontal (>0.5°, mean 1.5°) and the presence of low densities of worm tubes (<1000 individuals m^{-2}) near the break in slope to the low tide platform.

The beach face usually formed a firm slope that extended from the crest of the seaward beach ridge to just below or at the mean level of low water neap tides. The seaward margin was variable: in the winter months it extended onto the lowtide platform at the channel margin and during the summer months it retreated shoreward. Seasonal alteration of the level and extent of the slope were observed to relate to increased storm activity in the winter. The beach face was also altered during low tides by runoff channels from runnels and dewatering of the upper beach (Figure 3-7a).

The surface, exposed at most neap tides, was usually covered in small wave ripples, (8-10 cm chord, 1-2 cm height, mean ripple index:5) straight to undulatory and sub-parallel to the channel margin. At low spring tides the wave ripples often had superimposed small (current) ripples (7-12 cm chord, 1-3 cm height, mean ripple index:8) undulatory to linguoid, perpendicular to the wave ripples. Mud deposits in the troughs of linguoid small ripples were seen draped over wave ripples after an ebb spring tide under calm conditions. Projecting tubes were not aggregated in dense clumps on the beach face, but small groups of tubes and individual tubes were common at the low water neap level. Some patches of the Lanice tidal channel environment north of the study area were less protected from

waves, and wave bedforms developed on the low tide platform.

Rill marks, Eider browsing traces, and current crescents were common on the beach face. The rill marks were usually limited to runnel channels and ground water drainage, but did occasionally develop during late emergence sheet flow. Scour holes with slumps and deltaic run off systems developed from eider browsing activity but were quickly filled by wave swash. Current crescents formed with axes perpendicular to the shoreline around projecting tube tops and shells from wave swash. Algal cover was very light in the summer, usually limited to thalli attached to projecting tube tops and nonexistent in winter. Modification of surface features due to the presence of algae was negligible.

3.2.6.2 Small ripple field

Small ripple fields developed on most of the area of the low tide platform surrounding the other surface features. Some other divisions had small ripples superimposed on other features or bedforms but the small ripple fields were characterised by flat topography and primary small ripples (Figure 3-7b). The fields developed as discontinuous areas within other divisions and as a fairly continuous strip along the seaward margin of the beach face.

The surface was exposed at most spring tides although some discrete areas in the middle of the study area were only exposed at extreme low water spring. The surface was covered with straight, undulatory and linguoid, small ripples (6-20 cm chord, 1-5 cm height; mean ripple index: 7), perpendicular to the shoreline. Linguoid ripples were commonly seen at extremely low spring tides and on the relatively flat low tide platform that developed in winter.

Projecting tube tops were present as small clumps or strings parallel to the ripple axes and as isolated individuals. The density of tube tops varied a great deal but remained below 1000 tops m^{-2}.

Eider browsing traces, wader feeding traces, biogenic volcanoes and algal flow lineations were seasonally common in the small ripple fields. The surface was not as firm as adjacent divisions (except for pools) and was heavily worked for bivalves and polychaetes by oystercatchers, dunlin, herring gulls and terns. Eiders also disturbed the sediment and created shallow depressions that quickly filled on the incoming tide. Migration of small ripples over tube tops flush with the ripple troughs produced large areas with biogenic volcanoes. Algal thalli attached to tube tops and anchored to shells below the surface inhibited ripple migration in summer and produced distinctive flow lineations parallel to the shoreline.

Current crescents developed around shells and tube tops, particularly but not exclusively during late emergence sheet flow.

3.2.6.3 Algal-Lanice mounds

Algal-Lanice mounds developed subtidally in the channel floor and throughout the low tide platform in the summer (June-October). The tops of mounds were exposed during most spring tides and low neap tides. The bases of the mounds were only exposed at extremely low spring tides. They were a very distinctive feature and created a hummocky topography in contrast to the flat, small ripple fields and Lanice flats (Figure 3-8a).

The algal-Lanice mounds formed as undulatory mounds comprised of algal thalli and Lanice tubes. The surfaces of the mounds were marked by irregular algal flow lineations, ripple spurs and distinctive eider browsing traces. After periods of rapid sediment deposition, current crescents, small ripples and biogenic volcanoes developed on the irregular topography. The distribution of the mounds is believed to reflect the distribution of patches and linear arrays of tubes. These patches were generally orientated perpendicular to the dominant current direction (Figure 3-8b). Mounds invariably had tube top densities higher than 1000 top m^{-2} and a heavy cover of Enteromorpha sp. and or Polysiphonia sp. The Eider browsing traces were deep circular pits surrounded by vertical tubes and slumped sides and floored with collapsed tubes and algal debris. The relatively stiff mounds could retain the form of the pits for 2-3 days and on some occasions incorporated the depression into the stable mound. The areas between mounds were either small ripple fields or pools and a dynamic balance developed between the erosive effect of eider browsing and storm waves and the incorporation of sediment into stable mounds through settlement and growth of tubes and algal thalli.

Water level marks developed on the sides of mounds during some spring tides and were the only surface feature strictly limited to emergence. Eider browsing traces formed in very shallow (<0.5m) water.

3.2.6.4 Lanice flat

Flat areas composed almost entirely of close, evenly spaced tube tops of Lanice were developed in the summer months (June-October) and in some cases persisted through the winter to be rejuvenated in the spring. Although the flats were exposed only at particularly low spring tides on the low-tide platform they also extended onto the channel floor.

The surface of the flats was characterised by continuous areas with tube densities greater than 2000 tops m^{-2} and, in summer, by dense mats of algal thalli (Figure 3-9a). If the margins of the flats were level with the surrounding sediment (usually small ripple fields) they developed biogenic volcanoes through sediment influx. Water level marks, ripple spurs and Eider browsing traces developed on the margins that were substantially higher than the adjacent sediment.

Although the margins of the flats were difficult to distinguish from algal-Lanice mounds, the surface within the flats was quite distinctive. The tubes were regularly spaced in very firm, flat fields (Figure 3-9b). This surface was resistant to erosion and predation and sediment deposition was easily incorporated into the flat through tube extension.

3.2.6.5 Pools

Intertidal pools formed between groups of algal-Lanice mounds and along the margins of Lanice flats (Figure 3-10a). The raised surface of the mounds and flats retained water 1-30 cm deep, some of which drained off slowly in channels between the tube patches.

They were isolated as pools only during low spring tides but during many neap tides formed the largest area of shallow water on the low-tide platform. The pools were exposed to the entire range of physical disturbances of the sub-environment. The sediment was very soft and any surface features were very transient. Ripple fans described by Allan (1968) from the furrows of megaripples were the most common feature. The pools experienced intense predation and disturbance from plaice, dabs, eiders and waders.

Projecting tubes were rare and well dispersed ($<100\ m^{-2}$).

3.2.6.6 Drainage Channels

Shallow drainage channels formed between mounds and along margins of the flats during low spring tides (Figure 3-10b). The distribution of the channels was controlled by the areas of high relief and impounded water. These drainage channels are very similar in form to the runoff channels of runnels (King 1972), but were always associated with resistant masses of

tubes and in the study area generally flowed parallel to the shoreline.

The channels did not form sublittorally and only established a clear morphology at particularly low spring tides. The surface was composed of rill marks and rhomboid small ripples (5-10 cm chord, 1-2 cm height; mean ripple index 5). Micro deltas developed when the channels drained into standing pools or the embayment.

Few tube tops were exposed in drainage channels, those exposed were usually eroded from adjacent mounds or flats.

The drainage channels formed throughout the year when low tides combined with the irregular topography of the low tide platform. They are an excellent indication of subaerial exposure and when found in association with dense tube patches could mark the low spring tide level very accurately.

3.2.6.7 Islets

Islets formed by erosion of algal-Lanice mounds and Lanice flats developed on the low-tide platform from October until heavy settlement of Lanice in May-June. Their distribution was closely related to the distribution of the most substantial mounds and flats of the previous summer. They were found exclusively within small ripple fields and some of their characteristic features are associated with the current and sediment movement typical of that area.

Islet tops were exposed at all spring tides and at the lowest neap tides, the bases (and characteristic features) were exposed only on extremely low spring tides. Islets formed areas of high relief and firm substrate, although after periods of high sediment influx they were buried or flush with the adjacent surface (Figure 3-11a). The tubes forming the islets often had poorly developed "fringes" (see Chapter 6) but the formation of biogenic volcanoes indicated healthy worms within the mound. The islet's form developed in response to current erosion and assumed undulatory and rhomboid shapes similar to megaripples. The size varied greatly and their isolated distribution precluded description of a "mean ripple index". Height varied from 0-30 cm, with most islets forming mounds 10-20 cm high. Undulatory islets were 10-20 cm long along the current axis and up to 1 m wide across the current axis. Rhomboid islets were 15-30 cm long and 15-30 cm wide, usually diamond shaped with sub-equal axes. Islets with high relief (>15 cm) had fan-shaped small ripples, spurs and furrows around their perimeter (Figure 3-11b). Islets with low relief (<15 cm) had superimposed current ripples and biogenic volcanoes on lee and stoss slopes respectively.

Eider browsing and wave disturbance could severely disrupt the structure and persistence of the islets. If they survived through early spring (a time of intense browsing and wave activity) they provided the primary substratum for heavy settlement of Lanice juveniles. This process led to a reinforcement of the position of aggregations from season to season.

3.2.6.8 Megaripple field

Megaripples consistently developed at the channel margin of the study area and often developed on the channel floor. They were not observed along the exposed margins of all the observed patches. The megaripple field formed a small bar and enclosed embayment throughout the observations of the study area patch. This bar was composed of very soft sand and shelved steeply into the channel. Other patches had incipient megaripple fields without a steep slope into the tidal channel. The distribution and shape of megaripple fields was related to channel hydrography and they did overwhelm pre-existing Lanice flats, algal-Lanice mounds and islets. This migration only occurred when the channel geometry changed. A delicate balance was apparently maintained between algal-Lanice settlement and sediment stability. The presence of algal-Lanice associations may have starved potential megaripple fields of sediment and megaripple fields were too mobile to allow successful settlement of Lanice or algae.

The megaripple field was only exposed at the very low spring tides. It was composed of straight and undulatory, asymmetrical megaripples of 1-25 m chord and 10-60 cm height (mean ripple index: 33). The backs of the megaripples had superimposed linguoid small ripples and the troughs contained small ripple fans, spurs and furrows. On some occasions the megaripples developed deep scour pits which were modified by microdeltas and rill marks. The deep scour holes were associated with undulatory megaripples of height greater than 30 cm (ripple index:15) and were seen at the equinoctial spring tides (lowest, Figure 3-12b).

No tube tops or algal thalli were exposed on the surface of megaripple fields. The only biogenic surface structures were pits produced by bivalves (Spisula solida) as they left the sediment on the rising tides, and the marks left by waders, gulls and terns as they ate the bivalves (Figure 3-12a).

Large surface bedforms which would be classified as megaripples developed in other areas (chiefly small ripple fields and algal-Lanice mounds). These megaripples were low, straight structures (chord 1-5 m, height 10-20 cm; mean ripple index: 15) orientated northwest-southeast at an oblique angle to the shoreline. They influenced the shape of algal-Lanice mounds but appeared to be relatively stable features from tide to tide and formed a firm substratum. It is believed that these features were related to storm wave action or swell from the northeast rather than tidal currents because they formed predominantly on the beach margin on firm sediment and did not migrate during spring tides.

3.2.7 Distribution of divisions

The distribution of divisions of the Lanice tidal channel sub-environment within the study area was observed over a full year (March 1978 - March 1979). Particular attention was given to monitoring divisions associated with each sampling station on the transect throughout the sampling period. A summary of the transect data is presented in Figure 3-13. This represents a line transect through a complex of divisions and

must be considered with the distribution maps of the whole study area (Figures 3-5, 3-6).

The line transect observations allow recognition of transitions from one division to another. The discontinuous and biased nature of the observations (all made at extreme low water spring tides, > 5.1 m fall in water level) obscures many of the processes responsible for the transitions. It is necessary, therefore, to apply analytical methods such as those used to examine sedimentary rock units where the sediment deposition has been discontinuous.

Recent summaries of developments in the analysis of sedimentary rock units and their characteristics (sedimentary facies), have emphasised the value of "facies relationship diagrams" (Reading 1978, Walker 1979). These diagrams record the transitions from one facies to another, and whether the transitions are gradational (implying overlap of adjacent environments of deposition), or sharp (implying erosion or breaks in deposition, and possibly significant changes in the environment of deposition). They can be used to determine whether or not a particular transition occurs more often than would be expected from random alternations, and this may help in the recognition of genetic, successional or cyclic relationships (Reading 1978).

I have constructed a "division relationship diagram" outlining the observed transition frequencies between divisions (Figure 3-14). The small sample size limits the statistical value of this diagram, but it does permit a tentative framework to test against other observations.

Two parallel sequences or cycles are apparent, they are believed to reflect the two major structural forces in the sub-environment: algal-Lanice associations and current bedforms. The diagram records transition frequencies between small ripple fields, pools drainage channels and megaripple fields on the one hand, and small ripple fields, algal-Lanice mounds, Lanice flats and islets on the other hand. There may be an inter-relationship in the distribution of each sequence. Pools and drainage channels are controlled by areas of high relief at emergence (generally structures formed by algal-Lanice associations); and strong tidal currents, wave action and bedform migration can totally restructure the algal-Lanice associations. I have indicated postulated transition types on the diagram, these will be discussed further in Chapter 4.

Station 1 was on the beach margin of the Lanice sub-environment and experienced transition through four divisions. Settlement of Enteromorpha and Lanice on a small ripple field produced algal-Lanice mounds. Some of the mounds were orientated parallel to the shore, indicating modification from wave disturbance. The mounds were quickly eroded or buried to produce a small ripple field after the death of the Enteromorpha (September 1978, Figure 3-13). Further erosion and alteration of the beach during the winter resulted in the establishment of the beach face in this area. Drainage channels from the runnel temporarily covered Station 1 in September 1978 and may have contributed to the development of the small ripple field.

Station 2 had islets remaining from the previous year in March 1978 and these were successfully colonised by algal sporlings and Lanice juveniles resulting in the development of algal-Lanice mounds. No part of this area developed a Lanice flat but the mounds survived to March 1979 as islets. During February 1978 the islets were buried with sediment producing a small ripple field, and subsequently exhumed as an intact islet surface (Figure 3-13).

Station 3 developed into a substantial pool due to the high relief of Stations 2 and 4 and the surrounding topography (Figure 3-5). This pool developed from a small ripple field as the mounds developed around it. The drainage channel of this pool migrated across the station temporarily in October 1978. The pool was maintained throughout the winter in roughly its original position by the substantial islets that remained around it. Thus, this station was characterised by easily disturbed, mobile substrata throughout the study period.

Stations 4 and 5 were located within a large islet complex in March 1978. This complex was successfully colonised by Enteromorpha and Lanice and developed into a very substantial Lanice flat (Figure 3-5). Station 4 went through a transitional stage as an algal-Lanice mound and developed an erosion-resistant flat which persisted as a large islet through March 1978. Station 5 began as a more substantial islet, developed directly into a Lanice flat, but was eroded during the winter to a small ripple field.

Station 6 was a drainage channel in March 1978 but as the topography altered during mound growth, this channel migrated to Station 7. The area was heavily settled by Enteromorpha and Lanice and developed into substantial algal-Lanice mounds and then a Lanice flat. The Station marked the channel margin of Lanice settlement and was subsequently eroded to a small ripple field.

Station 7 remained on the margin of the megaripple field throughout the period of observation. The main drainage channel of the Lanice area migrated over Station 7 in May 1978. After January 1979 the channel migrated shoreward and megaripples were re-established at the station.

Stations 8-10 were within the megaripple field throughout the period of observation and experienced no transitions. Thus Stations 7, 8, 9, and 10 were all characterised by highly mobile sedimentological conditions.

Table 3-1

Characteristics of divisions of Lanice tidal channel sub-environment.

DIVISIONS	SURFACE FEATURES	CHARACTERISTICS
Beach face (B)	straight-undulatory wave ripples	shallow slope
	undulatory-linguoid current ripples	moderate tube density $<1000 m^{-2}$
	rill marks	<1000
	eider browsing traces (some)	
	light algal cover	
	current crescents	
Small ripple field (R)	straight-linguoid current ripples	flat surface
	wader feeding traces	moderate tube density $<1000\ m^{-2}$
	biogenic volcanoes	
	algal flow lineations	
	Eider browsing traces (many)	
	current crescents	
Algal-Lanice mounds (A-M)	undulatory mounds	hummocky
	algal flow lineations	high tube density
	ripple spurs	$>1000\ m^{-2}$
	Eider browsing traces	
	water level marks	
Lanice flat (L-F)	dense algal mats	flat surface
	Eider browsing traces (few)	very high tube density
	margins with similar features as (A-M)	$>2000\ m^{-2}$
Pools (P)	ripple fans	imponded water
		soft sediment
		very low tube density $<100\ m^{-2}$
Drainage channels (D-C)	braided rill marks	incised surface
	micro-deltas	slumps
	rhomboid ripples	rare tubes
	lag deposits	$<<100\ m^{-2}$
Islets (I)	tubes w/o fringe	isolated hummocks
	undulatory & rhomboid mounds	high tube density $>1000\ m^{-2}$
	spurs, furrows, ripple fans	
	linguoid small ripples	
	current crescents	
	biogenic volcanoes	
	no algal flow lineations	
Megaripple field (M-R)	straight-undulatory linguoid small ripples	
	spurs, furrows, ripple fans	megaripples
	scour pits	soft sediment
	lag deposits in pits	very low tube density
	no algal flow lineations	$<<100\ m^{-2}$

Figure 3-1

Lanice tidal channel sub-environment.

a. Surface of the sub-environment exposed during a low spring tide in September 1978. This view is to the northwest. The dominant ebb current direction was from the upper right to the lower left and the flood current direction was the reverse. Note the pools at the right and the left draining into the embayment in the foreground. The transect crossed this photograph from the upper left to the middle right, the centre of the photograph was the location of Station 4 (see Figures 2-3 and 3-5 for location of transect). Station 3 was in the centre of the pool on the left and Station 5 on the middle right margin of the photograph. Each transect station was 10 m apart.

b. Tidal channel margin of the sub-environment exposed during a low spring tide in September 1978. This view is to the west northwest and was taken from a point about 40 m east and 30 m north of Figure 3-1a. This photograph illustrates the abrupt change from the area dominated by settlement and growth of Lanice conchilega and algal species (dark area in middle) and the area on the margin of the tidal channel dominated by strong tidal currents and migration of megaripples (foreground).

Figure 3-2

Ripple profile diagram modified from Reineck and Singh (1975).

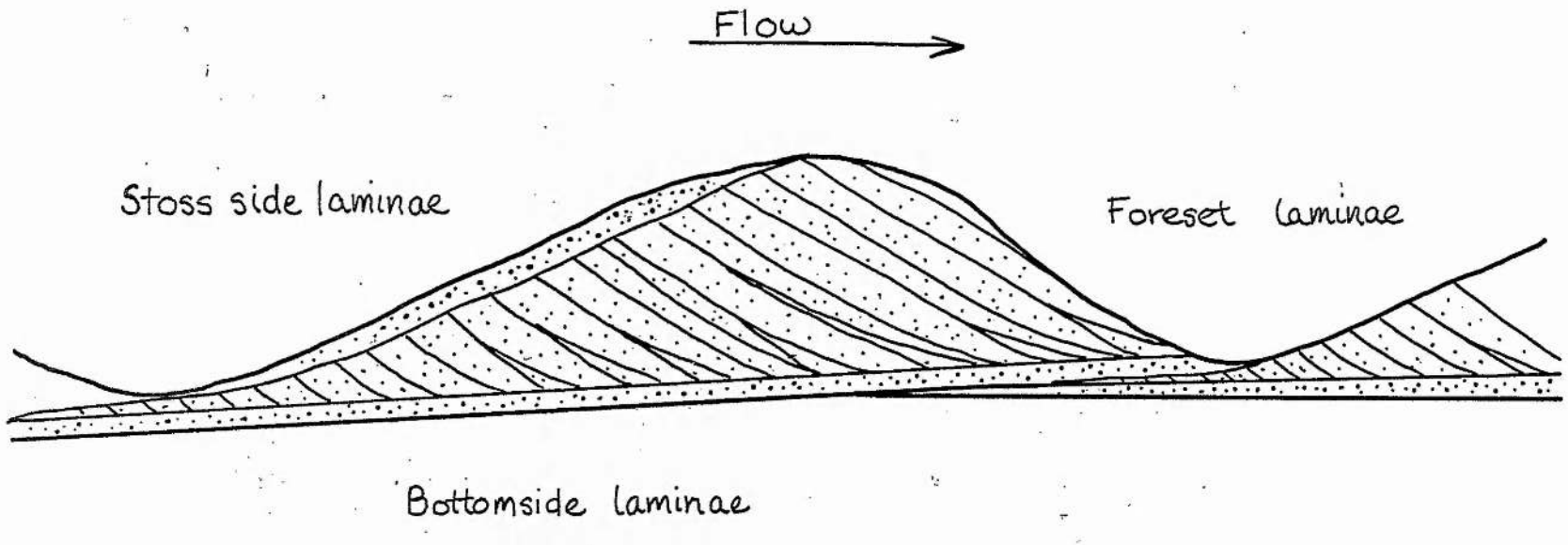

Flow
Stoss side laminae
Foreset laminae
Bottomside laminae

Figure 3-3

Recent Lebensspurren

a. Biogenic sand volcanoes formed by expulsion of mucous-laden sediment and water by Lanice conchilega. These structures are the result of migration of ripples across Lanice tubes. The worm expels sediment to clear the tube and a small mound forms around each tube. The volcanoes are composed of mucus-rich sediment and are resistant to erosion. As ripples migrate with the ebb and flood currents the volcanoes are alternately buried and exhumed. The ebb current flow direction was directly away from the camera. The camera lens cap is 48 mm in diameter. This photograph was taken during a low spring tide in May 1979.

b. Eider browsing trace formed by feeding activities of Eider ducks in shallow water. Ducks were feeding on high densities of Mytilus edulis spat attached to Lanice tubes. The ducks excavated a hole in the sediment with their feet and left a dish-shaped depression. The pool in this trace is about 30 cm wide and 5 cm deep. The waning ebb current has deposited drift algae in the trace and has transported a wedge of sediment across a Lanice flat to the edge of the trace. The ebb current flow direction was from the lower left to the upper right. This photograph was taken during a low spring tide in February 1978.

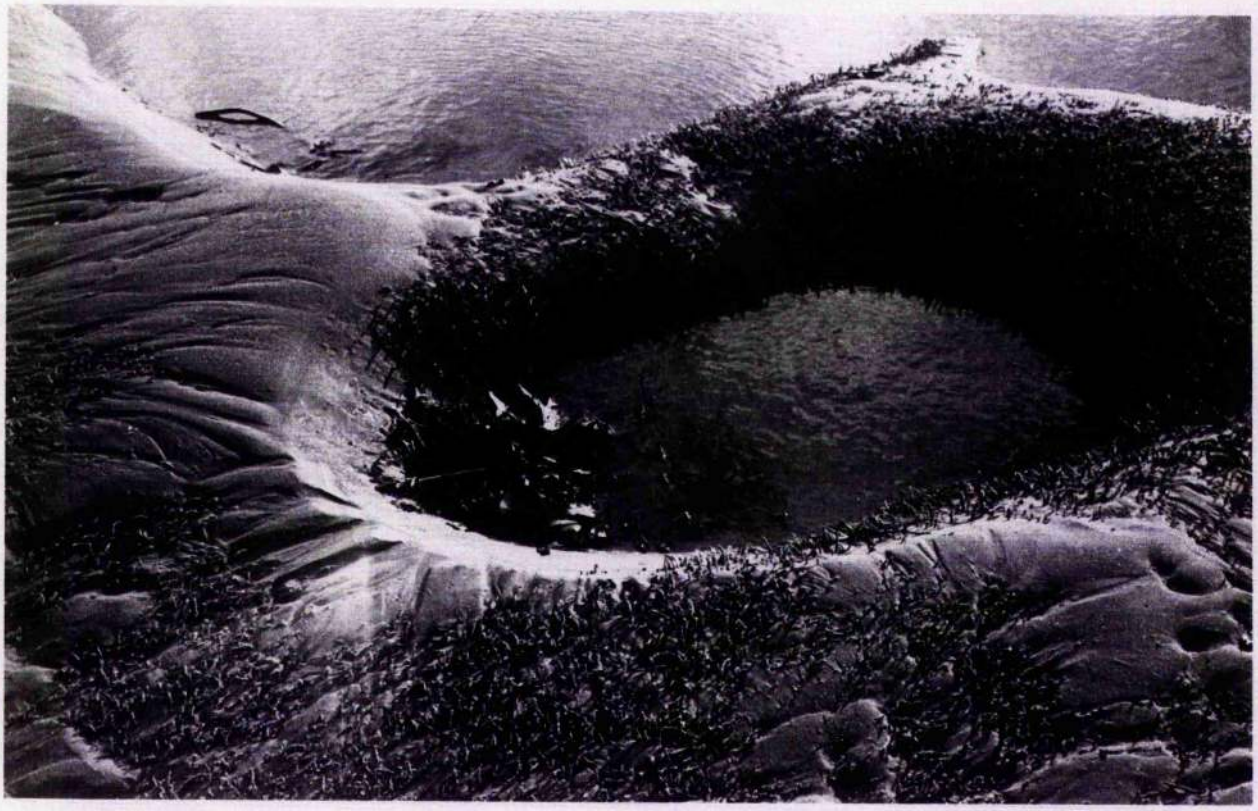


Figure 3-4

View of the transect looking east from Station 4 (foreground) to Station 9 during a low spring tide in September 1978. Station poles are 10 m apart. The foreground is a Lanice flat dissected by drainage channels and pools. The last three poles (7, 8, & 9) are in a megaripple field and the white area beyond them is the tidal channel. Two sand bars divided by another part of the tidal channel are visible on the horizon. This view should be compared with Figures 2-2 and 3-5 which are plan-view diagrams of the study area at this time (August 1978) and Figure 3-1a which is a view of the area in the foreground looking north during the same spring tide.

Figure 3-5

Distribution of divisions of the Lanice tidal channel sub-environment in August 1978

B-Beach face

R-Small ripple field

A-M-Algal-Lanice mounds

L-F-Lanice Flat

P-Pools

D-C-Drainage channels

M-R-Megaripple field

ELWS - extreme low water spring

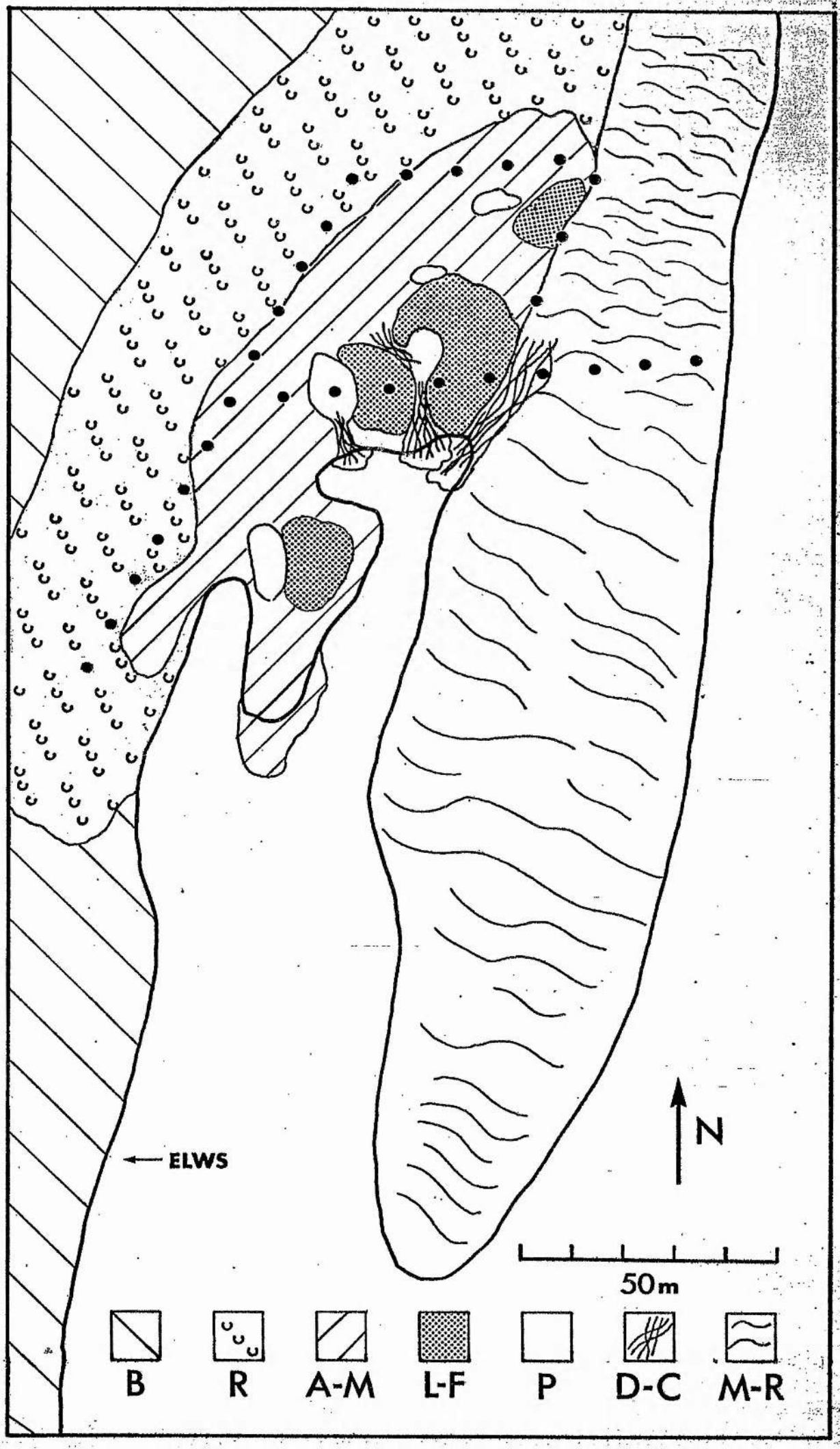

ELWS
N
50m
B
R
A-M
L-F
P
D-C
M-R

Figure 3-6

Distribution of divisions of the Lanice tidal channel sub-environment in January 1979.

B-Beach face

R-Small ripple field

A-M-Algal-Lanice mounds

L-F-Lanice Flat

P-Pools

D-C-Drainage channels

M-R-Megaripple field

I-Islets

ELWS-extreme low water spring

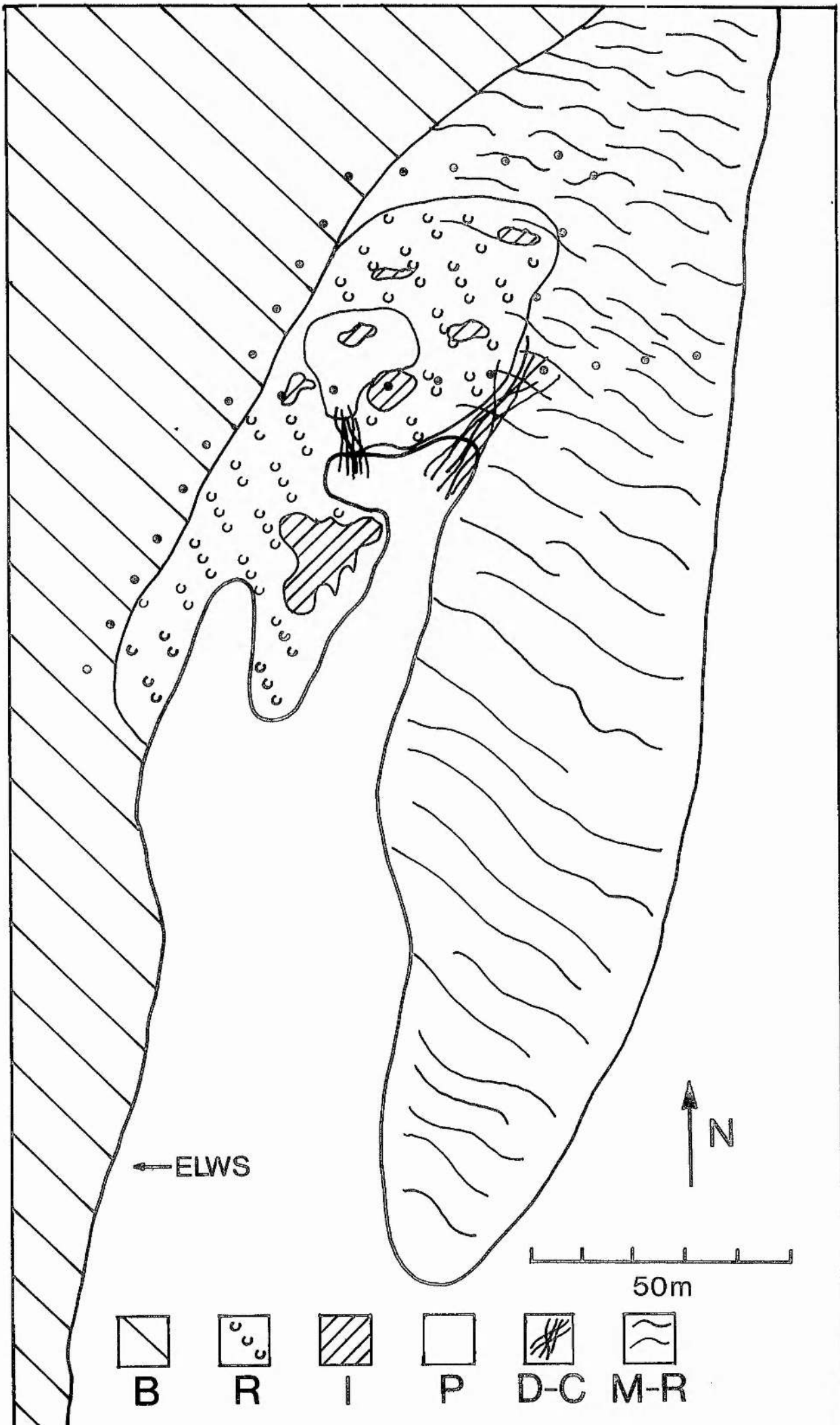

ELWS
N
50m
B
R
I
P
D-C
M-R

Figure 3-7

Beach-face and Small ripple Divisions

a. Beach face at the southwestern margin of the Lanice tidal channel sub-environment. The beach face has been altered by runoff from a runnel. The tower in the background is located about 250 m WNW of this point (see Figure 3-2 for location). This photograph was taken during a low spring tide in September 1978.

b. Field of small ripples. These undulatory ripples varied from 10-20 cm in chord and 2-5 cm in height. The ebb current direction was from the left to the right. The ripples are located on a larger bedform (the margin of this megaripple can be seen in the upper right) and formed during the ebb modification of the bedform. This photograph was taken during a low spring tide in February 1978.

Figure 3-8

Algal-*Lanice* mound Division

a. Algal-*Lanice* mounds at the northwestern margin of the study area. The tidal channel is on the right and the view is parallel to the dominant current direction (north). Note the orientation of the undulatory mounds perpendicular to the current direction (ebb flow was towards the camera and flood away from the camera). The dark area in the background is another large patch of the *Lanice* tidal channel sub-environment (see Figure 2-2 for location). This photograph was taken during a low spring tide in September 1978.

b. Algal-*Lanice* mounds in the middle of the study area. The beach face is in the background and the view is to the northwest. The three triangular objects in the left background are grid poles covered with drift algae. From the left they are poles 10, 11 and 12 respectively (see Figure 2-3 and 3-5 for location of the poles). The triangular object in the far right background is a broken salmon net pole and corresponds to the object in the middle left background of Figure 3-8a. The algal flow lineations provide an indication of the ebb current flow patterns (the dominant ebb direction was from the upper right to the lower left. The board in the middle right is 50 cm across. Note the distinct margin between the Algal-*Lanice* mound division and the small ripple field and beach face divisions in the background. This photograph was taken during a low spring tide in September 1978.

Figure 3-9

Lanice flat division

a. Oblique view of the surface of a dense Lanice flat. The surface was a solid mass of well-packed sediment, projecting tube tops and algae. The tube tops are so dense that the sediment surface is not clearly visible and individual tops are difficult to distinguish. The lighter, lacy clumps are tube tops and the dark stringy masses are dried algae. Just to the right of the lens cap is a mass of algal thalli and just above it is an individual tube top. The lens cap is 48 mm in diameter. Photograph was taken during a spring tide in September 1978.

b. Plan view of the surface of an adjacent area of the dense Lanice flat described above. Note the small (< 1 mm in the photograph) circular tube openings surrounded by branching fringe filaments. Light patches of sediment are visible to the left of the lens cap and at the upper margin of the photograph.

Figure 3-10

Pool and drainage channel divisions

a. Margin of an intertidal pool formed during emergence of the Lanice tidal channel sub-environment. The pool was an area of very low (< 100 m^{-2}) Lanice density surrounded by algal-Lanice mounds and Lanice flats. The tube tops visible on the algal-Lanice mound on the right were about 1 cm across. This photograph was taken during a spring tide in September 1978.

b. View looking north northwest of a drainage channel formed during emergence of the sub-environment. This drainage channel was a persistent feature and was located between station 4 and 5 during every spring tide in 1978. Storms disturbed the sub-environment in February 1979 and removed the tubes to the east of the drainage channel (right of photograph) and altered the runoff from the pool in the background. The channel was about 1 m wide in the middle of this photograph. This photograph was taken during a spring tide in September 1978.

Figure 3-11

Islet division

a. High relief islet with spurs and falling water marks. Ebb current direction was to the left. Islet had a height of 80 cm and chord of 500-600 cm. This photograph was taken on a low spring tide in October 1978. The layer of sediment on the crest of the islet was deposited during the ebb flow and notched by the falling water level. Note the ripple train on the stoss side (right foreground).

b. Ripple fan around low relief islet. Ebb current direction was to the left. Islet had a height of 10 cm and a maximum chord of 220 cm. This photograph was taken on a spring tide in May 1979. The wedge of sediment on the crest has migrated across the islet during the ebb runoff and migrated back during the first stages of flood.

Figure 3-12

Megaripple field division

a. Bivalves (Spisula solida) emerging from megaripple field during a spring tide. View to the north along the channel margin of the Lanice tidal channel sub-environment. These bivalves appeared to emerge when the tide changed from ebb to flood. The individuals in the lower left were about 5 cm long. Flood current direction is away from the camera. This photograph was taken during a very low spring tide in September 1978.

b. View of a large megaripple looking east along the transect. The pools are scour pits and the horizontal lines are falling water marks. The tidal channel is in the background. This view is the background of Figure 3-4 and here the station poles are 7, 8, 9 and 10 (respectively from the foreground) are visible. The station poles were 10 m apart and the ebb current flow direction was to the right.

Figure 3-13

Distribution of divisions of the Lanice tidal channel sub-environment along transect at each sampling time

B-Beach face

R-Small ripple field

A-M-Algal-Lanice mounds

L-F-Lanice Flat

P-Pools

D-C-Drainage channels

M-R-Megaripple field

I-Islet

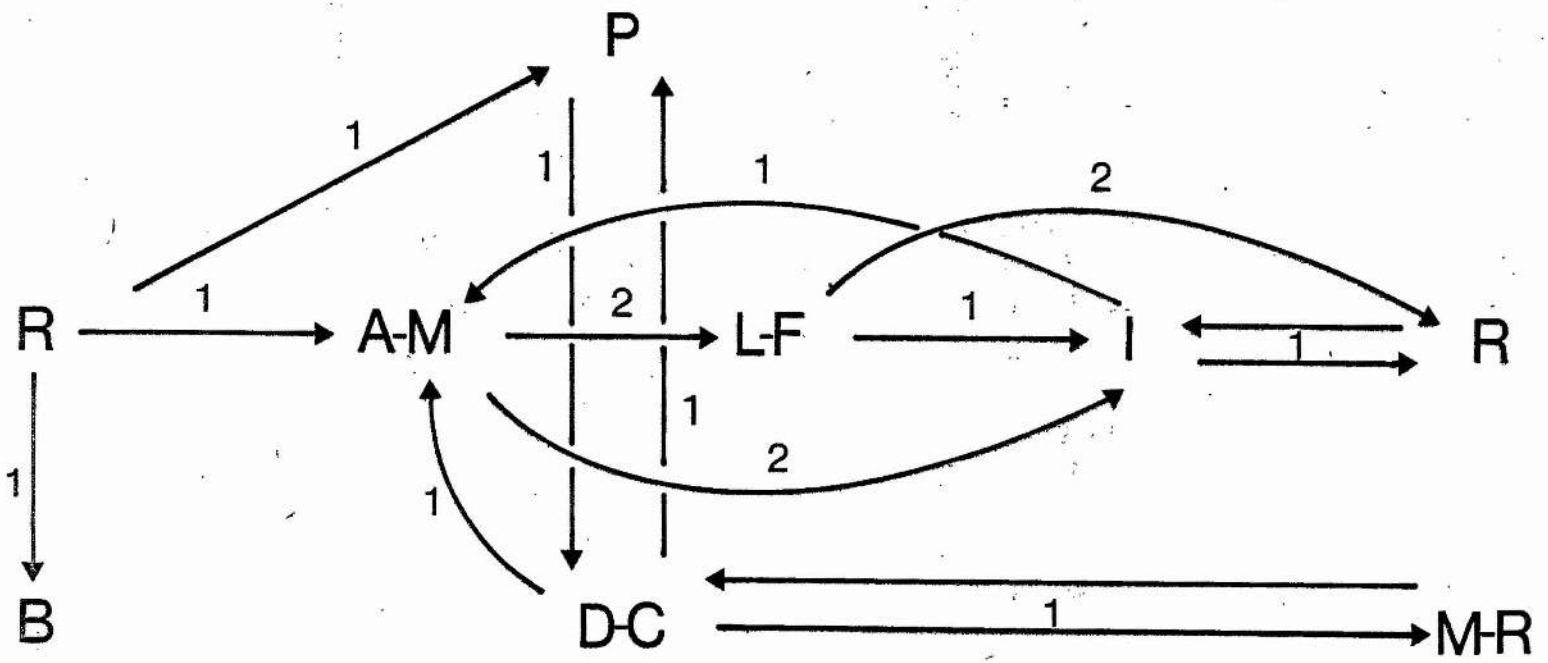

P
1
1
1
2
R
1
A-M
2
L-F
1
I
1
R
1
1
2
1
B
D-C
1
M-R

Figure 3-14

Diagram illustrating the relationship between divisions of the Lanice tidal channel sub-environment. Based on field observations and derived from "facies relationship diagrams" (Selley 1970, Walker 1979). Numbers represent the frequency of observed transitions.

B-Beach face

R-Small ripple field

A-M-Algal-Lanice mounds

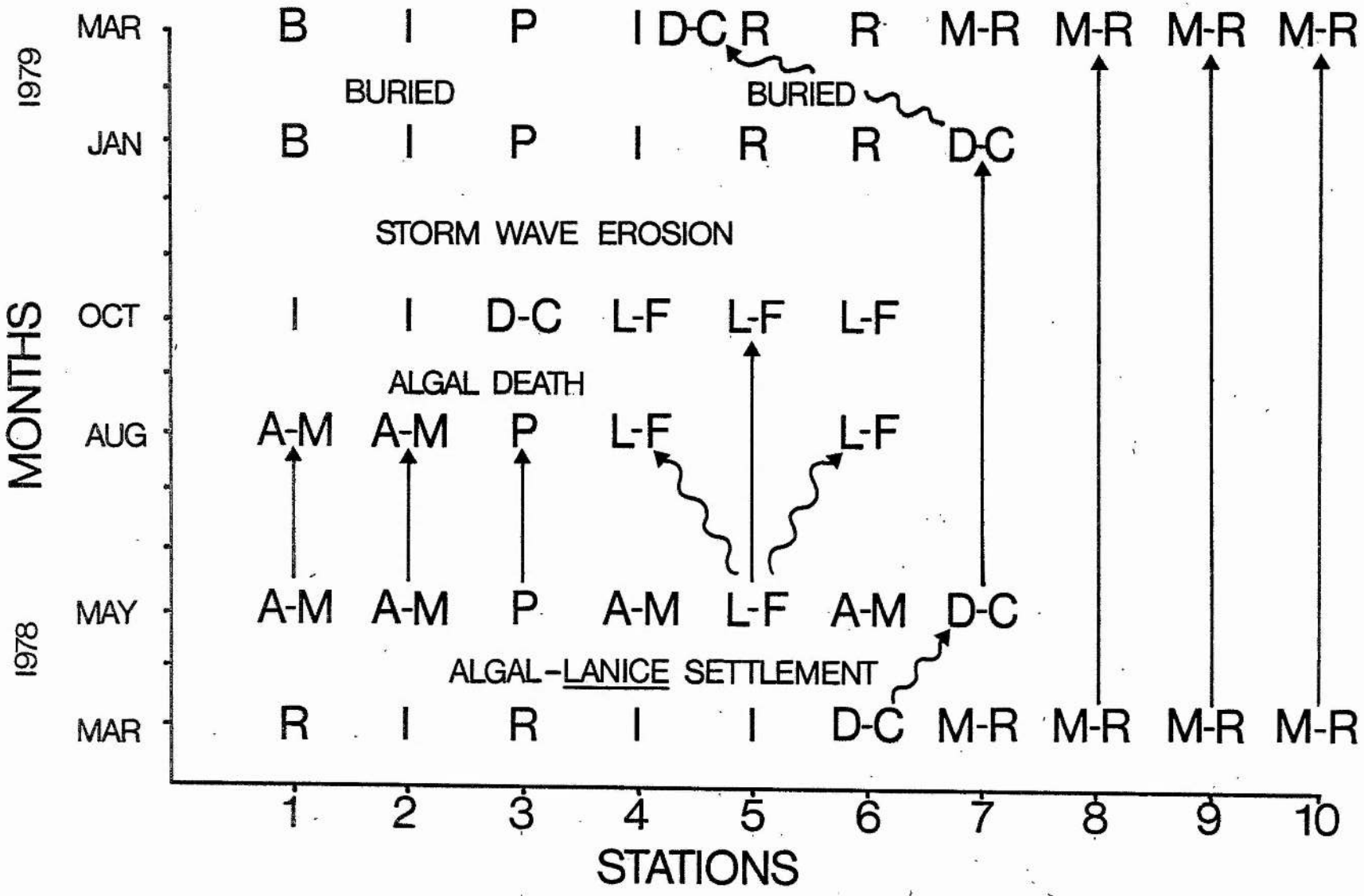
L-F-Lanice Flat

P-Pools

D-C-Drainage channels

M-R-Megaripple field

I-Islet


MAR
1979
JAN
OCT
AUG
MAY
1978
MAR
MONTHS
B I P I D-C R R M-R M-R M-R M-R
BURIED
BURIED
B I P I R R D-C
STORM WAVE EROSION
I I D-C L-F L-F L-F
ALGAL DEATH
A-M A-M P L-F L-F
A-M A-M P A-M L-F A-M D-C
ALGAL-LANICE SETTLEMENT
R I R I I D-C M-R M-R M-R M-R
1 2 3 4 5 6 7 8 9 10
STATIONS

4 Chapter 4 Sedimentological analysis

4.1 Grain-size characteristics

Sediment characteristics averaged for all samples taken at Tentsmuir are listed in Table 4-1. The average sediment at Tentsmuir was a fine sand with a moderately well-sorted, negative-skewed, mesokurtic grain size distribution. This sediment corresponded to Eastwood's (1977) Textural Facies I, which he described from South Tentsmuir and other parts of the lower Eden Estuary. Eastwood (1977) differentiated textural facies on the basis of a cluster analysis of raw weight percentage data obtained by sieve and pipette analysis. He reported an average fine sand fraction of 73 weight %, a clumped category (very coarse sand, coarse sand and medium sand) which he termed "medium sand" of 23 wt %, and a very fine sand fraction of 2.71 wt %. The grain size distribution of this textural facies, however, was nearly symmetrical and leptokurtic; it was also better sorted than that of the Tentsmuir sediments studied here (Table 4-1).

Eastwood (1977) concluded that the sediments of his Textural Facies I were transported and deposited in a high energy environment dominated by tidal currents with subordinate wave action. He inferred from the experimental results of Moss (1972) that the development of a particular bedform in this facies is related entirely to the hydraulic regime, and that the grain-size places no restrictions on bedform development.

Details of sample collection and treatment are in Appendix I. Samples were collected from transect stations in August 1978 and April 1980, sub-samples from August 1978 were analysed for calcium carbonate ($CaCO_3$) content by weight. To facilitate comparison with previous sedimentological studies in the area (Green 1974 1975, Eastwood 1977, McManus et al. 1980), grain size distributions have been presented as the graphic analogues of Inman (1952) and Folk and Ward (1957). The graphic measures are: the Mean (M_Z Ø), which provides a measure of average grain size; Sorting (Inclusive Standard Deviation, $_I$ Ø) a measure of dispersion analogous to the standard deviation of conventional statistics; Skewness (SK_I Ø); and Kurtosis (K_G Ø). These measures allow description of the sediments based on the central 68% of the sediment grain population (McManus et al. 1980).

The two sampling periods represent extremes in the distribution of divisions of the sub-environment. The period of August 1978 was characterised by extensive development of algal-Lanice mounds; 4, 5 & 6 were Lanice flats with dense algal mats; 3 was a pool; 7 a well-developed drainage channel between the flats and the megaripple field of 8, 9 & 10. The period of April 1980 was characterised by current bedforms with little or no modification of sediment by Lanice and no algae present. The surface at this time was a very flat, small ripple field merging with a megaripple field at the channel margin with no sharp division. Islets were present at 1 & 2 and were flush with the sediment surface and over-ridden by small ripples. This surface topography is consistent with other observations made after storm activity. No islets were actually located on the transect, so two samples were taken in areas with tubes present: in an

islet, S_1; and in a small ripple field, S_2.

Although carbonate sedimentation in high latitude, temperate regions is considered unimportant by many geologists, apart from localised areas of high concentration (Milliman 1974), the presence of small amounts of recognisable carbonate fragments can be a valuable guide to biological and sedimentological processes in areas of primarily detrital sedimentation. The study area at Tentsmuir was an area with relatively high bivalve density, a high density of animal tubes selectively composed of carbonate fragments and rich in biogenic sedimentary structures marked by fluctuations in the density of carbonate fragments. For these reasons it seems appropriate to consider the provenance and identity of the carbonate fragments in these sediments in some detail.

The calcium carbonate content by weight of the sediments on Tentsmuir Beach was generally > 3% (Eastwood 1977, this study Table 4-1). This fraction was mainly composed of shells and fragments of bivalves, gastropods, echinoids and frequent barnacle plates. Zenetos (1980), in a thorough study of the distribution of living and dead molluscs in the Eden Estuary, suggested that the relative density (or biomass) of dead molluscs played an important rôle in the contribution of calcium carbonate to the sediment in this area. Furthermore, Zenetos (1980) differentiated four biotopes on the basis of Q-mode cluster analysis of living and dead mollusc assemblages in the Eden and concluded that they were consistent with Eastwood's (1977) textural facies. Biotope I occupied the area of South Tentsmuir Beach (as did Textural Facies I) and was distinguished by the presence of bivalves associated with the open beaches and sand flats.

Green (1975) described seven sub-environments based on sediment characteristics, sedimentary structures and the distribution of organisms, live and dead from three localities on the southern entrance to the Tay. None of his sub-environments is directly comparable to the Lanice tidal-channel sub-environment, but his results can provide information on the distribution of sediment and potential sources of calcium carbonate. The location of Green's (1975) localities, Zenetos's (1980) Biotope I, Eastwood's (1977) Textural Facies I and the area discussed here are shown on Figure 4-1.

Table 4-2 summarises the distribution of genera of living and dead organisms from each area that might have contributed calcium carbonate to the sediments. Primary sources of living molluscs are the Eden Estuary, the tidal channel, Tayport Beach, and sublittoral populations in St. Andrews Bay. Barnacle plates (Balanus) are contributed from the rocky intertidal areas near St. Andrews, drift seaweed and the surface of mussels (Mytilus edulis) from the Eden and Tay estuaries. Echinoderm tests and fragments come from the sandy sublittoral areas of the bay. Shells and fragments are transported by wave and current action, wind and predators. Transport of shells by predators is often neglected, but waders, gulls, ducks and seals consume large numbers of bivalves and can deposit faeces composed almost entirely of shell fragments (Pounder 1971). The migration of these predators from one feeding ground to another can transfer fragments of mud-flat species to beaches and vice versa.

The distribution of the shells of one particular species reflects the confusion that can result from erosion and transport in severe storm conditions. Lutraria lutraria is a large (15-20 cm length) eulamellibranch bivalve which was reported by McIntosh (1875) as "common in muddy sand at mouth of Eden". No live specimens have been reported from any locality in St. Andrews Bay since that time. Large numbers of valves are common, however, after storm activity along Tentsmuir Beach (Green 1975, and this study), in the Eden and the West Sands (see Figure 4-1 and Table 4-2). Lutraria may be present sublittorally as this area has not been extensively surveyed, or the valves may represent a relict population which is periodically exhumed and cast onto the beaches by storm waves. In either case the distribution of the dead shells is clearly not a reliable indicator of present population distribution. However, the accumulation of the valves in channel lag deposits and on storm beaches can overwhelm the contribution, by weight, of all other species living or dead.

Despite the potential source of confusion through transport, the distribution of shell fragments, valves and tests in the study area closely reflects the living populations (Table 4-2). Mytilus (mussel) occurs in the area only as spat, but the feeding activity of Eiders can transport shell fragments from Tayport Beach and the inner Eden Estuary (see Section 5.3.3 and Pounder 1971). Barnacle fragments occur throughout the sediments of Tentsmuir Beach and the West Sands and are presumably transported by predation and storms, as the sources are very remote from Tentsmuir. The nearest source is the surface of mussels in the Tay Estuary and the Eden Estuary both about 4.5 km from the study site; the nearest rocky intertidal source is at St. Andrews about 8 km from the study site (Figure 2-1).

Echinocardium (sea urchin) tests are frequently cast onto the beaches in very large numbers by storm waves and their spines and fragments of the plates contribute to the "medium" sand fraction of the sediments.

The Lanice tidal channel sub-environment is an area of relatively high densities of a wide range of bivalve species. The valves of dead individuals, and fragments from animals in other sub-environments provide a rich source of carbonate sediment particles. These particles accumulated in lag deposits and algal-Lanice associations. The accumulations may have formed because of hydrodynamic factors (lag deposits) and active selection of flat fragments as tube-building material by Lanice. The interrelationship between the presence of lag deposits of shell fragments and the preference of Lanice for this material in tube building was not investigated.

The settling velocity and behaviour of carbonate fragments is different from that of rounded quartz grains. Due to their irregular, usually plate-like shape, bivalve shell fragments have a lower settling velocity than quartz grains (Braithwaite 1973) or spheres of equivalent diameter and density (Maiklem 1968). Their variable shape and density generally preclude any assumption of hydrodynamic equilibrium with the main sediments (quartz sand) based on sieve analysis. Eastwood (1977) excluded all carbonate particles larger than the coarsest lithic fragment and determined the carbonate fraction in each size grade by weight. He concluded that in most of his outer estuary samples the size distribution of carbonate assumed a similar shape to the total sediment distribution. In samples from the middle estuary and the southern end of the tidal channel studied here, the carbonate fraction was concentrated in the coarse

and very coarse sand size-grades. Eastwood (1977) suggested that this coarse "tail" is due to local production of carbonate fragments and does not allow the assumption of hydrodynamic equilibrium.

The carbonate fraction from this study was generally evenly distributed throughout the size-grades (Table 4-1). Observations indicated, however, that in many samples the very small pebble (-1.0 phi), very coarse sand (0.0 phi) and coarse sand (1.0 phi) grades were almost entirely composed of carbonate. These samples correspond to the areas dominated by algal-Lanice associations (4,5,6, August 1978) and islets ($1,2,S_1$, April 1980) and may reflect the predilection of Lanice for coarse, flat particles in tube construction (Wunderlich 1970), as well as the distribution of lag deposits within tube-dominated areas.

4.1.1 Distribution of sediment characteristics

The mean grain size in almost all of the samples along the transect (Stations 1-10) was within the Wentworth (Griffiths 1967) fine sand grade (2.0 - 3.0 phi). Stations 4, 5 and 6 were coarser than this (medium sand grade 1.0 - 2.0 phi) in August 1978 (Figure 4-2). The samples which had $CaCO_3$ removed (August 1978, see Appendix I) had a smaller mean size at 4, were larger at 6, 8, 9 and 10 and show no change at 1, 2, 3, 5, and 7. This demonstrates the highly variable content of the "coarse tail" sediments in the algal-Lanice associations. Stations 1 and 2 had a smaller mean grain size in August 1978 and showed no change in the sample with $CaCO_3$. These stations had over twice the average weight % in the very fine

sand grade and this may reflect increased exposure to wave action. Eastwood (1977) found similar concentrations of the very fine sand size grade on the West Sands and concluded that it was due to swash action driving very fine sand into the beach.

The samples from April 1980 although exposed to considerable wave action (flat topography, buried islets), did not show an increase in the very fine sand sub-population, but rather a decrease in both the medium sand sub-population and the very fine sand size grades and an increase in the fine sand size grade relative to the August 1978 sample (Table 4-1). The effect was to decrease mean grain size overall, relative to August 1978 with a clear trend of decrease from beach to tidal channel margin. Lanice tube density had no apparent effect on this trend as samples S_1 and S_2 fall on the trend and had greater tube densities than the transect samples (Figure 4-2).

The graphic sorting scale (inclusive standard deviation) is independent of the mean and shows the spread of grain sizes in terms of the Wentworth grades (Griffiths 1967). The sediments had an average sorting value within Folk's (1968) moderately well-sorted division (0.51 - 0.70 phi). Samples 4, 5 and 6 of August 1978 were only moderately-sorted and samples 1 and 2 of August 1978 were well-sorted (Figure 4-3). The samples which had $CaCO_3$ removed (August 1978, see Appendix I) showed a similar change in sorting relative to intact samples (August 1978) as they did for mean grain size. Sample 4 was better sorted without $CaCO_3$; 6, 8, 9 and 10 showed a decrease in sorting; 1 and 7 showed no change and 2, 3 and 5 were slightly better sorted (Figure 4-3). This again indicates the presence of a "coarse tail" of $CaCO_3$ in sample 4, less so in 2, 3 and 5; a "fine tail"

of $CaCO_3$ in 6 and less so in 8, 9 and 10.

The post-storm sample set (April 1980) is, on average, better sorted than the algal-Lanice sample set (August 1978) and shows a steady increase in sorting from the beach margin to the tidal channel margin. This is not affected by the density of Lanice tubes (see S_1 and S_2 in Figure 4-3).

The graphic phi skewness measure is dimensionless and independent of the phi sorting measure (McManus et al. 1980). It is a measure of the location of the sediment distribution on a fine to coarse scale with negative values indicating the peak of the distribution is skewed towards the finer grades. At the Tentsmuir study area, the sediments, on average, had a negative-skewed distribution. This negative skewness was due to a coarse tail, primarily composed of carbonate but also including coal, lithic fragments and man-made particles (brick glass). Samples 4 and 5 were more strongly negative-skewed, and sample 2 much more nearly symmetrical than the other samples (Figure 4-4). These departures from the normal values were reduced in the samples without $CaCO_3$. The samples from post-storm conditions (April 1980) were, as might be expected, more nearly symmetrical in the distributions than the samples from the summer conditions. The trend in these samples (April 1980) is not pronounced but appears to become more symmetrical towards the tidal channel margin. The density of tubes in April 1980 had no apparent effect on the skewness measure (see S_1 and S_2 in Figure 4-4).

Kurtosis is a measure of the dispersion in the tails of the distribution compared with that in the central portion (Folk 1968). It is difficult to interpret meaningfully and is included here for purposes of comparison only. The distribution of kurtosis showed no clear relationships along the transect. Values ranged from 0.74 - 1.38 and the average value was 1.09 in August 1978 and 1.02 in April 1980. Most values remained with the verbal description "mesokurtic" (Folk 1968). Eastwood (1977) gives an average value of 1.20 (leptokurtic) for his Textural Facies I, elsewhere (p. 115) he states, however, that the sediments of South Tentsmuir Beach and the ebb- and flood-tidal deltas are mesokurtic.

Carbonate content of the sediments increased in the dense algal-Lanice associations (Figure 4-5). Stations 4, 5 and 6 had a higher $CaCO_3$ content in August 1978 than the average value of 5.27 %. Stations 3 and 7-10 had decreasing $CaCO_3$ content toward the channel margin, and 1 and 2 about the average.

The clumped `medium sand' category of Eastwood (1977) obscures the importance of the coarse tail, present in my samples but largely absent in his. This coarse tail of the grain-size distribution produced the reduction in sorting and the negative skewness values observed in the samples from my study area. The tail was primarily composed of carbonate particles, but not entirely because the samples with carbonate removed still showed negative skewness values (Table 4-1).

This effect is also seen in Table 4-3 which presents the raw weight percentage data for all size classes for the August 1978 samples. From this table we can infer the carbonate composition of each size fraction (the size distribution was not measured before removal of the carbonate). The sample without carbonate still has a coarse tail but shows a considerable loss in weight percent in the coarse fractions (-1.0 - 1.0) as well as the very fine sand fraction. The apparent gain in the medium sand (2.0 phi) and fine sand (3.0 phi) fractions is not in weight, but in relative importance because of the use of percentage rather than absolute weight.

The coarse tail was more prominent in samples taken from areas dominated by Lanice tubes. It is not known whether this was a direct result of Lanice activity (alteration of hydrodynamic conditions near the bed, active collection of coarse particles for tube building materials) or if the presence of these coarse sediments and the related hydrodynamic conditions influenced the settlement distribution of Lanice. What is clear is that in this area with a source of carbonate particles and minor amounts of coarse sediments, the presence of dense beds of Lanice and local concentrations of coarse carbonate and detrital particles are closely related.

4.2 Internal structures

Investigation of subsurface physical and biogenic sedimentary structures has been one of the most useful methods of relating modern and ancient depositional environments (Bouma 1969, Howard 1978). Ideally, cores of sediment from each division of the sub-environment should be available for comparison with results from lithified deposits. Singlehanded collection of large, intact cores and preparation of *in situ* peels requires long periods of exposure (2-4 hours). The number of adequately low spring tides which would have made this possible at Tentsmuir was not sufficient to allow a full collection of fauna, sediments, cores , observations and photographs. However, cores were obtained from: islets, *Lanice* flat, algal-*Lanice* mounds, and megaripples. The following discussion of sediment structure incorporates results from these cores, observations in the field and evidence from similar depositional environments elsewhere.

Box cores were used to collect intact, rectangular cores of unconsolidated sediments for analysis of sedimentary features within the sediments. Cores were collected with a large Senckenberg - type sample box (Bouma 1969). A box 40 cm x 30 cm x 7.5 cm was constructed to collect large, deep profiles of sediments and *Lanice* tubes. The tubes often extended over 40 cm vertically into the sediment, but it was found that 40 cm was the practical depth limit for collection of complete cores. They were used for two purposes: to prepare relief peels of internal sedimentary structures, and to investigate sub-surface orientation of *Lanice* tubes.

Cores were treated by the method of McMullen and Allen (1964) to preserve structures in relief with polyester resin. Intact cores initially were treated in the field and removed to the laboratory for the final drying process. Peels were prepared by levelling the surface of an open-faced sample box (McMullen and Allen 1964, and Bouma 1969), covering the surface with folded gauze, and evenly pouring the resin mixture on the surface. The resin mixture consisted of 85 parts Mitchell and Smith's Polymaster 761 liquid epoxy resin (supplied by Bondaglass-Voss Ltd., Beckenham, Kent), 15 parts monomericstyrene, 4 parts Butanox M-50 (catalyst) and 2 parts 1% Cobalt Naphthanate (accelerator). After hardening (48 hours at 20° C) the sample was placed, cloth side down, on a piece of hardboard and the excess sand removed by washing. Cores prepared by the method produced peels of 2-5 cm thickness with high relief.

Cores used to investigate sub-surface orientation of Lanice tubes were treated by washing (Ziegelmeier 1969). Cores were placed on a slight incline with the cover removed and a mesh screen over the lower end of the box. The core was carefully rinsed with seawater to remove the sediment. Positions of tubes were noted as successive layers were removed and later reconstructed on hardboard for photography.

Peels of sediment cores can provide a record of short-term sediment deposition and the activity of organisms. Two representative peels will be discussed below: one with evidence of current bedforms with little influence from organic activity, the other dominated by organic activity.

4.2.1 Physical Structures

As water and sediment move over a current ripple, sediment is deposited in three main areas: the shallow angle stoss-side, the steep slipface, and the trough (Reineck and Singh 1975 and Figure 3-3). Deposition in these area produces respectively: stoss-side laminae, foreset laminae and bottomset laminae (Figure 4-6). Stoss-side laminae are rarely preserved, foreset laminae dip steeply (up to 35^{o}) in the direction of flow and the horizontal bottomset laminae extend underneath the ripple from trough to trough (Reineck and Singh 1975). Reversal or variation of tidal current flow direction produces "reactivation surfaces" (Collinson 1970, Klein 1970) and may reverse the orientation of the bedform with concomitant reversal in dip of the foreset laminae.

Boersma and Terwindt (1981) described in great detail the effects of neap and spring tidal cycles on the development of internal structures of large current ripples in a mesotidal estuary. They refined the terminology regarding reactivation surfaces and distinguished three sets of structures related to sediment transport models, current measurements and observations of large ripple movement. These structures are termed: reactivation structures, full vortex structures and slackening structures. They are respectively interpreted as: acceleration of flow, full development of bedform migration, deceleration of flow. My observations, although limited to low spring tides only, are consistent with their results. The peel illustrated in Figure 4-7 was taken from the crest of a megaripple during a low spring tide. This peel represents only a small portion of the whole structure, but its features can be related to larger peels presented by

Boersma and Terwindt (1981).

The lower portion of the peel (AA´-BB´) is a small wedge-shaped section of large foreset laminae formed on the flood-tide, by avalanche of bedload down the lee-side of the megaripple. There is an erosional "pause plane" (BB´) followed by small ebb-orientated foresets which may represent migration of small ripples across the megaripple after high slack water. There are five small "cosets" (BB´-CC´) of small ripple foresets truncated by a pause plane (CC´). These are followed by gently dipping laminae which probably represent deposition from traction (CC´-DD´) or bottomset laminae. With a presumed increase in ebb flow velocity the ebb crest or cap of the megaripple developed fully and avalanche foresets were formed (DD´-EE´).

It is not clear from this small section whether the megaripples were symmetrical, flood or ebb-orientated. Boersma and Terwindt´s (1981) results have indicated that large-scale bedforms from mesotidal estuaries are complex structures which can show considerable variation on tidal and neap-spring scales. If their interpretations are applicable to the tidal channel at Tentsmuir it is likely that the megaripples are flood orientated during spring tides and the sequence seen in Figure 4-7 could represent deposition during a single tidal sequence. On this basis the structures would be interpreted as follows. AA´-BB´: remnant of full-vortex stage flow in the flood direction. BB´: erosional pause plane formed during the first part of ebb acceleration stage. BB´-CC´: reactivation structures formed during ebb full-vortex stage. DD´:pause plane followed by slackening structures formed during deceleration stage and further modification on emergence.

4.2.2 Biogenic structures

Bioturbation refers to disruption of primary sedimentary structures by the activities of organisms. The recognition of these primary biogenic structures and their environmental significance is considered an important tool in the interpretation of sedimentary strata (Seilacher 1964, Howard 1975, Rhoads 1975). Biogenic structures are usually abundant in depositional areas protected from physical disturbance and rare or absent in depositional areas dominated by physical forces. In general, the degree of bioturbation increases rapidly with increasing water depth (Howard and Reineck 1972); increases in a seaward direction along estuaries (Howard et al. 1975, Howard and Frey 1975) and sharply decreases at the entrance to estuaries and in the intertidal zone (Howard and Reineck 1972, Howard et al. 1975). The observable drop in preserved bioturbation at estuarine entrances and intertidal areas is attributed to wave reworking and repeated erosion and deposition of sediment (Howard 1978). Careful examination of biogenic structures can, in some cases, reveal a detailed history of intermittent deposition and erosion (Goldring 1964). Vertical structures (e.g. mucous lined tubes, packed sediment in burrows) are truncated by erosion and may be extended through layers of rapidly deposited sediment. Very rapid sedimentation may smother the infauna and a new assemblage will be established on the new surface.

Parallel laminated sand layers disrupted by bioturbation have been observed widely in nearshore sediments (Reineck and Singh 1971, Howard and Frey 1972, Wunderlich 1971, 1972, Reineck 1977). Parallel laminated sand is attributed to wave activity on exposed coasts (e.g. Oregon coast,

Clifton et al. 1971) and storm activity on more protected coasts (Gulf of Gaeta, Reineck and Singh 1971 and Sapelo Island, Howard and Frey 1975). Howard (1972) and Howard and Frey (1975) recognised a cyclic sequence of: erosional contacts, laminated sand layers, increased bioturbation upwards, followed by an erosional contact. Howard (1972) reported a preserved sequence of this type (from the Upper Cretaceous of Utah) and suggested that it was formed by alternate periods of storm and non-storm conditions in an environment at or just below wave base.

Lanice builds tubes with three sections: the buried shaft, the protruding trunk and on it the fringe crown. The walls of the buried shaft are composed of in situ sediment particles bound by mucus and internally strengthened. The projecting trunk is constructed grain by grain of sediment particles and if available flat shell fragments, echinoderm spines, gastropod shells and Foraminifera tests. The large (1-10 mm) fragments are frequently orientated parallel to the sediment surface and perpendicular to the axis of the tube (Wunderlich 1970, Schäfer 1972). A branching fringe is also carefully constructed of selected particles around the projecting trunk (Schäfer 1972, Ziegelmeier 1952, 1969). If the tube is buried, the worm burrows to the surface, cementing a cylindrical tube shaft as it goes, and constructs another trunk and fringe. In this way, sequences of rapid deposition may be recorded despite subsequent bioturbation, if the difference between in situ particles and selected particles is apparent. Myers (1970) reported a similar record in the tubes of Diopatra cuprea.

Adult Lanice usually construct a single, vertical tube but newly settled larvae burrow in a U-shape before constructing a fringe. As the worm grows it breaks out through the tube near the bend and constructs a new tube parallel to the old tube (Seilacher 1951, Schäfer 1972). The process appears to occur frequently in some circumstances: Ziegelmeier (1952) suggested lack of food, competition for food,oxygen depleted water, dense byssal mesh of Aloidis gibba as possible causes; I have observed worms in the laboratory building tubes as a means of locomotion (see Fauchald and Jumars 1979 for other examples) and others actively maintaining two fringed trunks. Lanice is clearly capable of spacing tubes, abandoning blocked or unsuitable tubes and recovering from extensive erosion or deposition.

The peel illustrated in Figure 4-8 was collected from the crest of an islet in February 1978. The peel represents a vertical section orientated parallel to the dominant flow direction and perpendicular to the elongated islet. This peel is representative of peels collected from algal-Lanice associations and reflects cycles of erosion, deposition and the activity of infaunal animals and algal thalli.

Four distinct horizons are discernible on this peel (Figure 4-8). AA´ traces a line of shell debris and horizontal tube fragments indicating an erosional surface. Below this line the vertical tubes are armoured with shell fragments and tubes that pass through it are shell covered below the line and sand covered above it (Sh-S). Above the sand tubes other shelly tubes appear and continue to BB´. BB´ is also marked by shell debris and displaced tubes and above it the tubes are distinctly sandy (Sh-S). The

tubes are shelly above CC´ indicating a stable surface horizon (S-Sh). This level is also marked by decaying algal thalli (T). The wedge-shaped area of sediment above CC´ was deposited on an ebb tide before emergence of the islet and contains a suspension feeding bivalve (Donax vittatus) in life position (D). The top of the peel (CD´) was the exposed sediment surface at the time of collection.

All horizons in this peel exhibit some relict lamination (L) and bioturbation. The depositional sequence is interpreted as follows. The lowest horizon (up to AA´) was an eroded surface of an algal-Lanice mound: note the inclined laminae (L) on the left with horizontal tube fragments on the erosional surface and bioturbation on the right with vertical shelly tubes. The eroded surface was buried by fine sand. A tube assemblage developed within the sand through extension of tubes from below and construction of new tubes. Sediment accreted relatively slowly around this dense assemblage of tubes: note the long shelly tube shafts, relict laminae on the right, and bioturbation throughout. Larval settlement occurred on a surface near BB´: note juvenile tubes (J). BB´ marks another erosional surface rapidly buried by at least 10 cm of fine sand: note parallel laminae (L) and tube extensions (Sh-S). A new surface was established at CC´. This surface is marked by algal thalli (T) that probably extended from a lower horizon (BB´). The presence of the algal thalli may have restricted erosion of this surface: note shelly tubes projecting from an inclined surface, this may represent the stoss-side of a flood modified algal-Lanice mound. This surface was subsequently buried with fine sand on an ebb tide and the surviving worms re-established contact with the new surface.

The horizon between BB′ and CC′ was slightly anoxic below the decaying algal mat while the layer above CC′ was very fresh uncompacted sediment. The anoxic layer is marked by black sand (bl) and the fresh oxidised sediment by light brown sand (br). This evidence suggests that the surface CC′ has been buried previously (restricting oxygen circulation below dense mat), exhumed and re-buried. CC′ was probably the previous summer surface, buried in the autumn, exhumed in winter storms and subjected to burial under migrating wedges of sand when the core was collected. This conclusion is supported by surface observations: the islet was of a form similar to Figure 3-11b with a wedge of sediment visible on the ebb slipface. These wedges of sediment have been observed to begin to move across the islets as ripple trains on the flood tide. The migration of sediment alternately exposed and buried groups of tubes, which can result in biogenic volcanoes (Figure 3-3a).

The suggestion that CC′ was a summer surface, experiencing moderate cycles of erosion and deposition is also supported by the presence of a U-bend between AA′ and BB′. This U-bend has been interpreted as an escape structure from an eroded or buried tube. Lanice usually breaks through an old tube as near the base as possible and constructs a parallel tube to the surface. The position of the U-bend should be about 30 cm below the surface for large adult tubes (>3 mm diameter), if this was the case here, CC′ would represent the approximate original surface of the abandoned tube.

The washed core in Figure 4-9 was collected from a large algal-Lanice mound in July 1978. The removal of sediment exposed a buried surface (AA´) about 12 cm below the exposed surface (BB´). The buried surface (Figure 4-10) is marked by algal thalli (T), tube fringes (F) and juvenile tubes (J). The juvenile tubes recovered in this core are U-shaped and attached to the adult tubes in clumps of up to 15 individuals. Many of the fragile juvenile tubes were broken or lost on washing but they, as well as the adults and the algal mats, extended their tubes or thalli through a layer of sediment to the exposed surface (Figure 4-9, BB´). The buried surface of Figures 4-9 and 4-10 is comparable to the preserved erosional surface BB´ in Figure 4-8, and to a surface can-cored in July 1978. 33 adult Lanice and 258 juvenile Lanice were present in 0.08 m^2 of the July 1978 surface and 102 adults and 220 juveniles were present in 0.08 m^2 of an adjacent surface (Appendix Table II). The adjacent surface was buried with sand and the tubes were only visible as holes and biogenic volcanoes.

Seilacher (1951) was the first to recognise the possible value of Lanice-like tubes as trace fossils. Ziegelmeier (1952, 1969) and Wunderlich (1970) expanded on Seilacher´s observations and these are ably reviewed in Schäfer (1972). Meyers (1970) described a similar, large agglutinated tube (of Diopatra cuprea) and speculated that it might also have value for interpretation of fossil traces. Tubular aggregations of foraminiferal tests (Roniewicz 1970) and crinoid ossicles (Ettensohn 1981) have been described as fossil agglutinated tubes. At least one of these (Crininicaminus haneyensis, Ettensohn 1981) has been attributed to annelids. Chamberlain (1971a) described a trace fossil very similar to the tubes of Lanice (Lanicoidichna metuluta), from sand horizons over shale in

the Wapanucka Limestone (Pennsylvanian) of Oklahoma. This trace has a U-bend and aggregated tubes 2-7 mm wide, and 60 cm long. It has also been tentatively identified in a channel sandstone over shale in the Joana Limestone (Mississippian) of Utah (Gutshick and Rodriguez, 1977).

Table 4-1

Average sediment characteristics for all samples
Range is shown in brackets below average
See Appendix I for information on sample collection and treatment.

Raw Weight Percentage

	August 1978 with $CaCO_3$	August 1978 without $CaCO_3$	April 1980	Textural Facies I Eastwood (1977)
"Medium sand" -1.0-2.0 phi	24.99 (4.96-46.62)	26.30 (3.51-41.83)	18.08 (3.75-40.41)	23.07 (3.46-66.74)
Fine sand 3.0 phi	71.80 (51.14-87.65)	71.86 (56.21-91.36)	81.06 (58.32-92.60)	73.20 (33.00-91.00)
V. fine sand 4.0 phi	3.20 (1.24-7.38)	2.26 (0.88-4.74)	1.69 (0.80-3.64)	2.71 (0.50-8.60)
$CaCO_3$ loss		5.27		

Folk and Ward Statistics (1957)

	August 1978 with $CaCO_3$	August 1978 without $CaCO_3$	April 1980	Textural Facies I
Mean	2.24 (1.85-2.51)	2.23 (2.05-2.50)	2.36 (2.08-2.50)	2.29 (1.83-2.65)
Sorting	0.63 (0.39-1.03)	0.59 (0.34-0.80)	0.48 (0.33-0.64)	0.42 (0.27-1.18)
Skewness	-0.2442 (-0.4131-+0.1118)	-0.2484 (-0.3561- 0.000)	-0.1781 (-0.2656- 0.000)	0.0000 (-0.320- +0.410)
Kurtosis	1.09 (0.85-1.38)	0.98 (0.74-1.17)	1.02 (0.74-1.26)	1.20 (0.83-5.16)

Table 4-2

Occurrences of living (L) and dead (D) animals likely to contribute carbonate to sediments. Locations of sampling sites shown on Fig 4-1.

Zenetos Biotope I	Carey Lanice-tidal channel	Green Tentsmuir beach	Green Tentsmuir point	Green Tayport beach
Bivalve Molluscs				
Tellina(L/D)	Tellina(L/D)		Tellina(D)	Tellina(L)
Donax(D)	Donax(L/D)			
Venus(D)	Venus(L/D)			
Mytilus(D)	Mytilus(D)	Mytilus(D)	Mytilus(D)	Mytilus(L)
Spisula(D)	Spisula(L/D)			
Macoma(D)	Macoma(D)	Macoma(D)	Macoma(D)	Macoma(L)
Cerastoderma(D)	Cerastoderma(L/D)		Cerastoderma(D)	Cerastoderma(L)
Solen-Ensis(D)	Ensis(L/D)	Ensis(D)	Ensis(D)	
Abra(D)				
Lutraria(D)	Lutraria(D)	Lutraria(D)	Lutraria(D)	
Ostrea(D)				
Nucula(D)				
Thracia(D)	Thracia(L/D)			
Barnea(D)				
Hiatella(D)				
Arthropods				
Balanus(D)	Balanus(D)			
Echinoderms				
Echinocardium(D)	Echinocardium(D)			

Table 4-3

Difference in raw weight percentage for each phi class between samples with carbonate and those with carbonate removed.

	Phi class					
Sample	-0.1	0.0	1.0	2.0	3.0	4.0
August 1978 with carbonate	0.52	0.91	4.38	19.18	71.80	3.20
August 1978 without carbonate	0.08	0.34	3.83	22.06	71.86	2.26
Percent Difference	84 loss	63 loss	12 loss	15 gain	.08 gain	29 loss

Figure 4-1

Location of descriptive sediment/organism studies.

Green (1975): Tayport Beach, Tentsmuir Point Beach, Tentsmuir Beach

Present study: Lanice tidal channel sub-environment

Zenetos (1980): Biotope I

Eastwood (1977): Textural Facies I

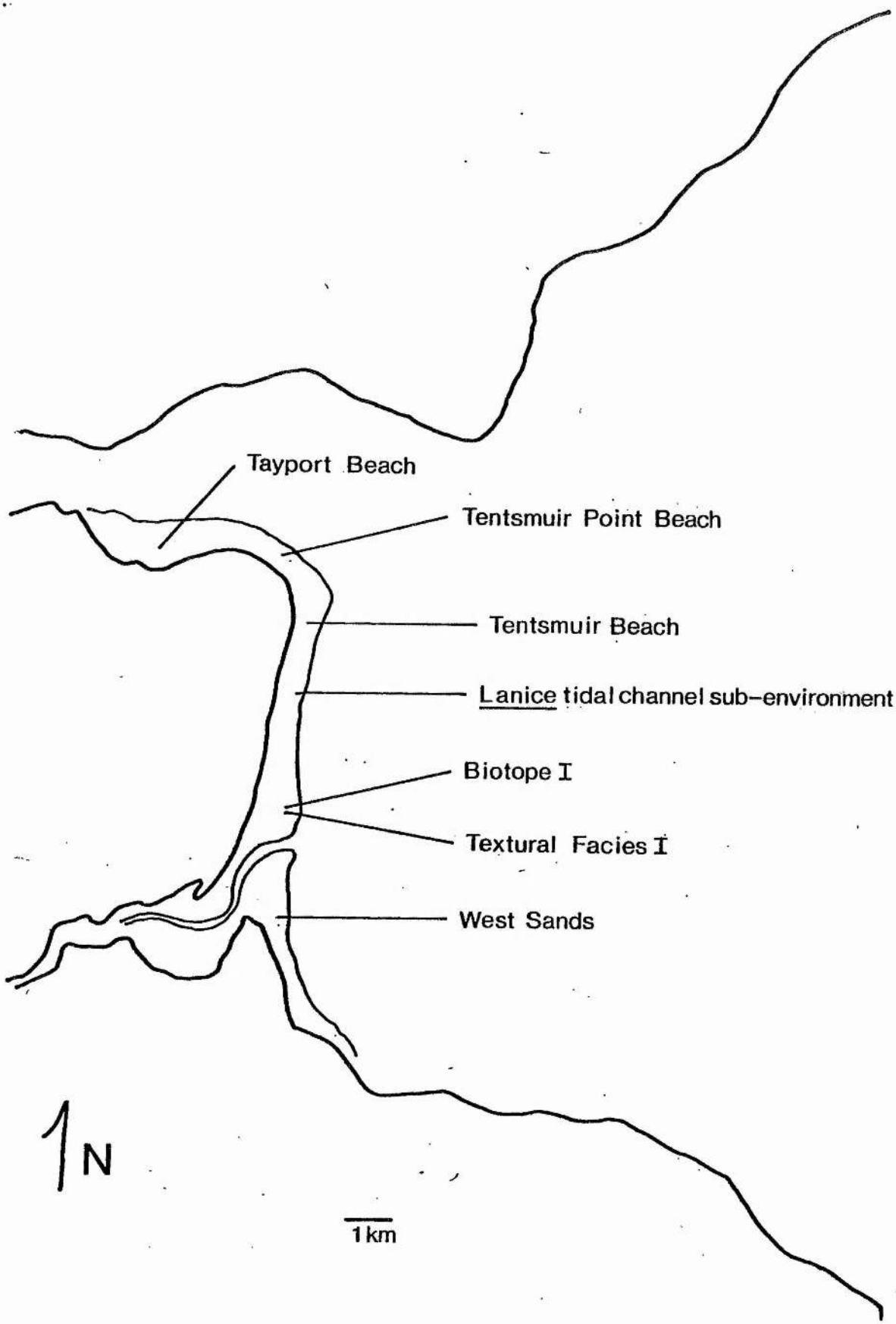

Tayport Beach
Tentsmuir Point Beach
Tentsmuir Beach
Lanice tidal channel sub-environment
Biotope I
Textural Facies I
West Sands
N
1km

Figure 4-2

Graphic mean grain size for sediment samples collected along the transect at Tentsmuir Beach. See Appendix I for details of sample collection and treatment and Appendix Figure I for location of sampling sites.

GRAPHIC MEAN GRAIN SIZE

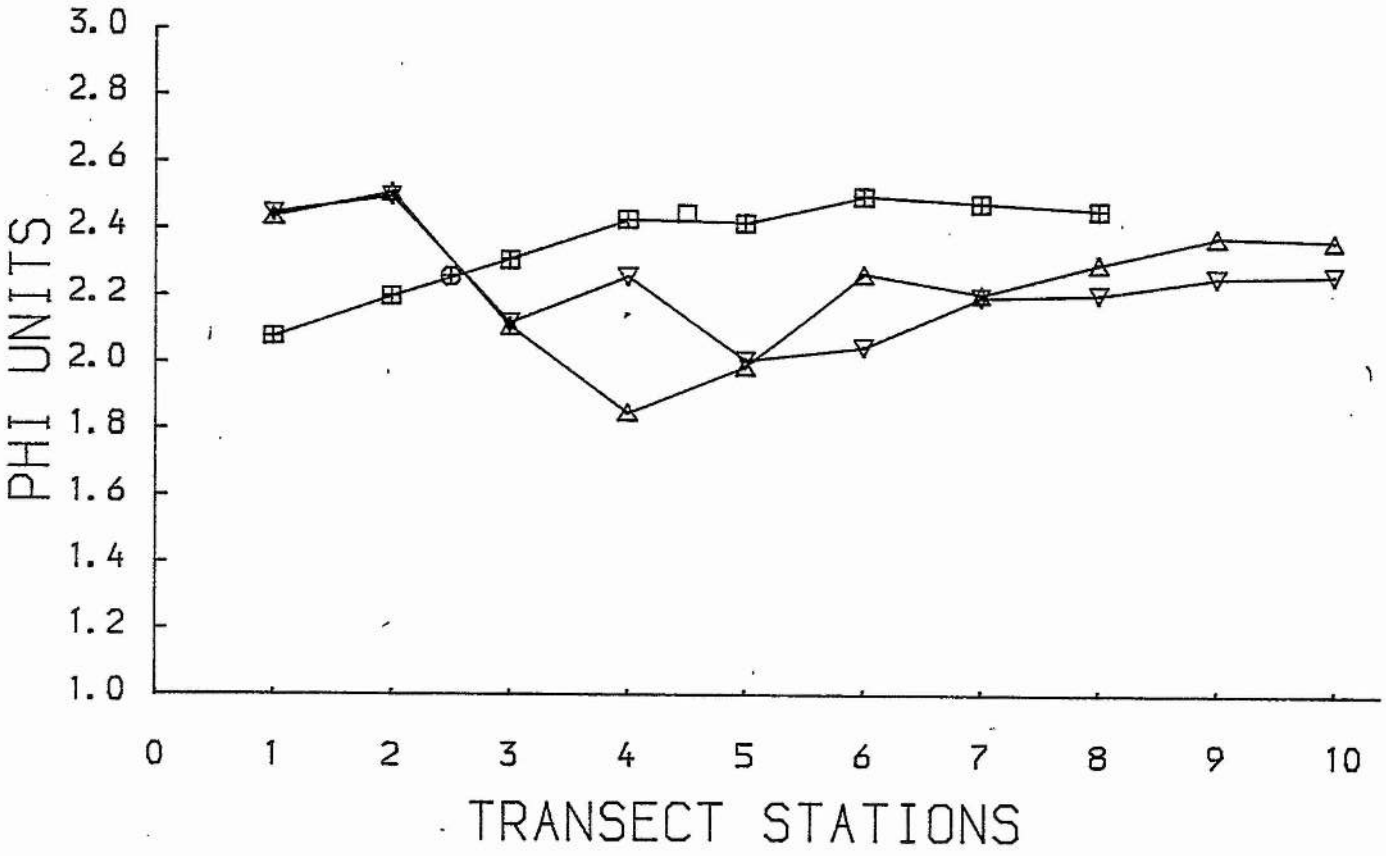
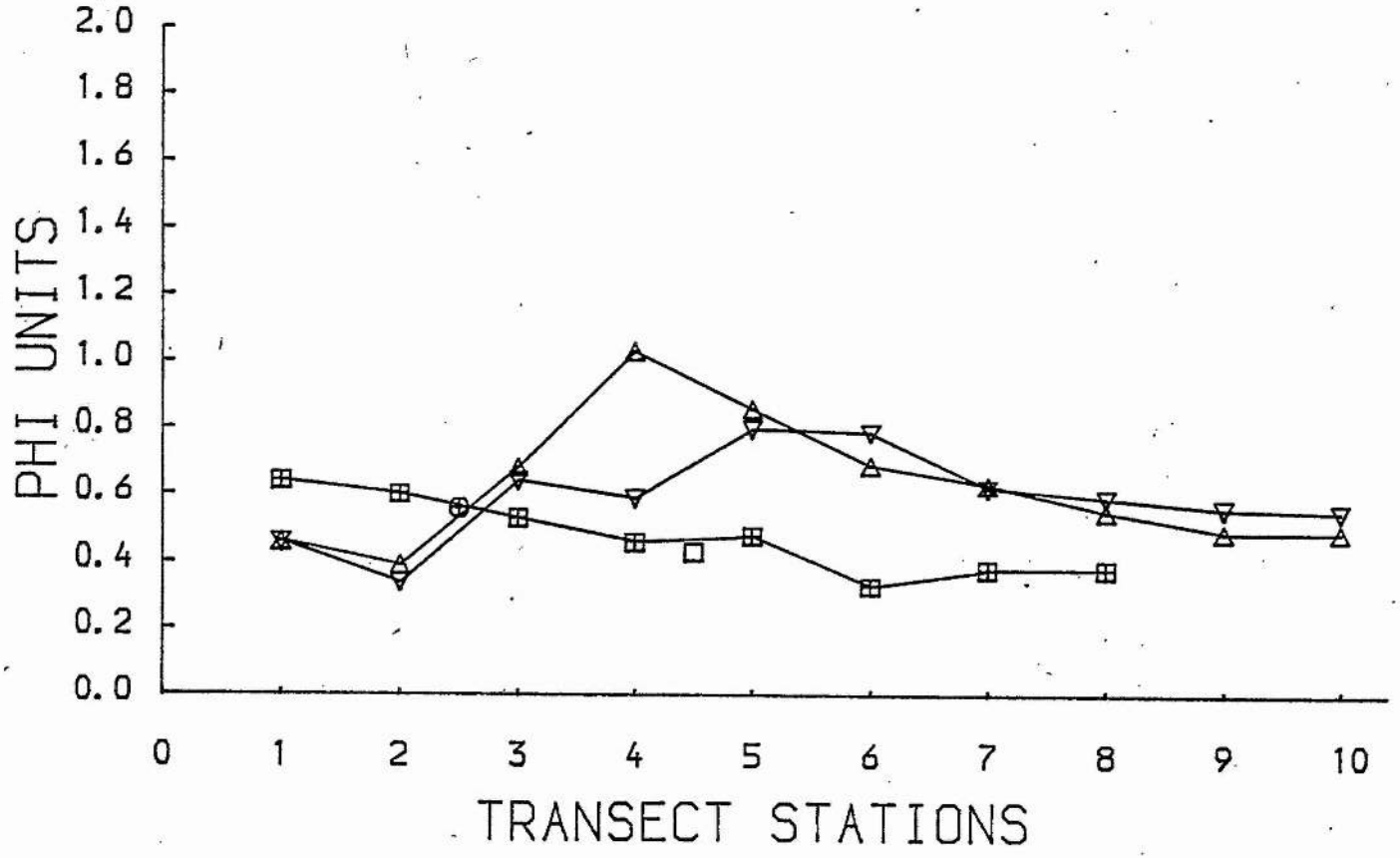


Figure 4-3

Graphic sorting in phi units for sediment samples collected along the transect at Tentsmuir Beach. See Appendix I for details of sample collection and treatment and Appendix Figure I for locations of sampling sites.

GRAPHIC SORTING



△ AUGUST 78 w/ CaCO3 □ APRIL 80 S1

▽ AUGUST 78 w/o CaCO3 ⊕ APRIL 80 S2

⊞ APRIL 80

Figure 4-4

Graphic skewness for sediment samples collected along the transect at Tentsmuir Beach. See Appendix I for details of sample collection and treatment and Appendix Figure I for location of sampling sites.

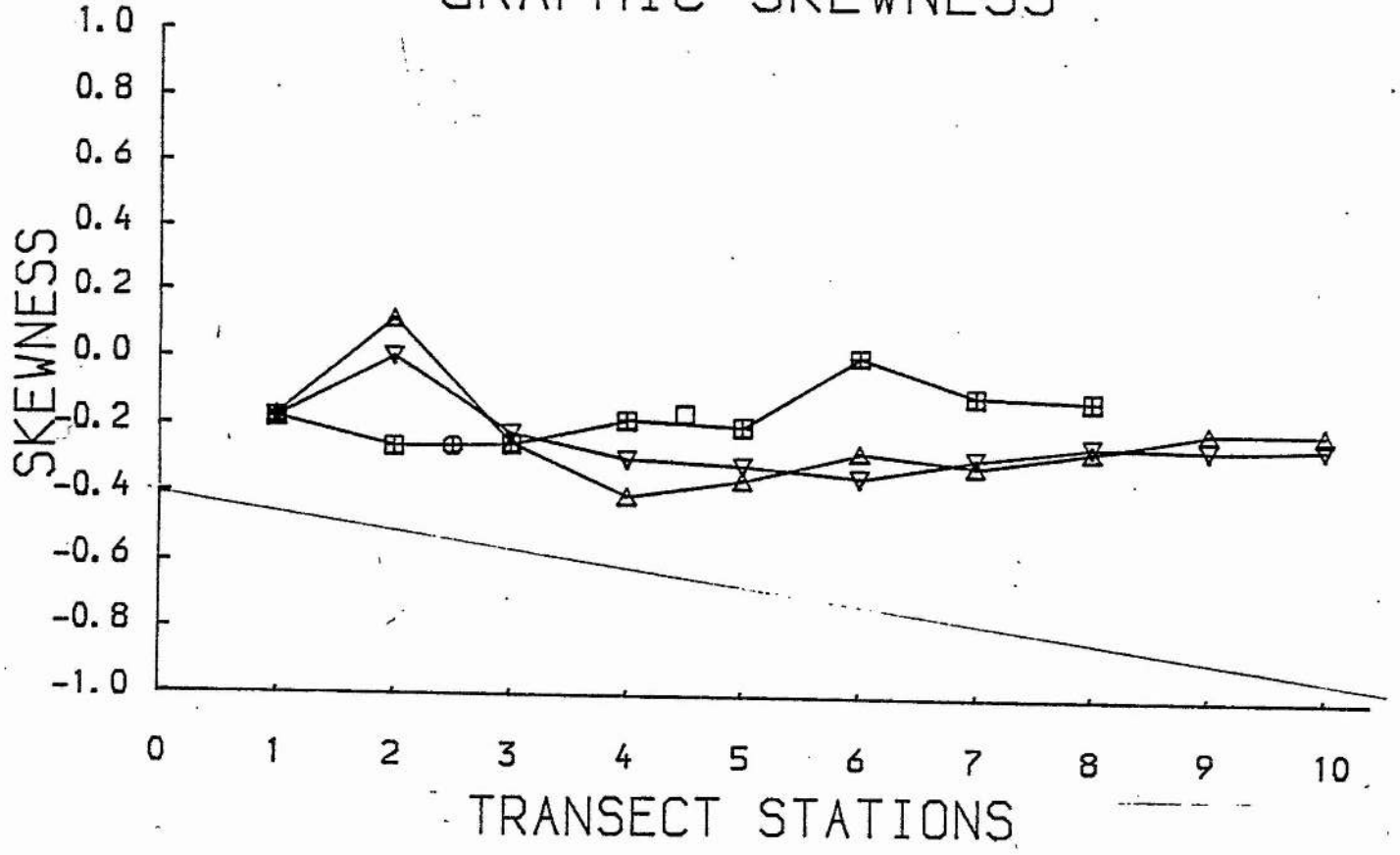
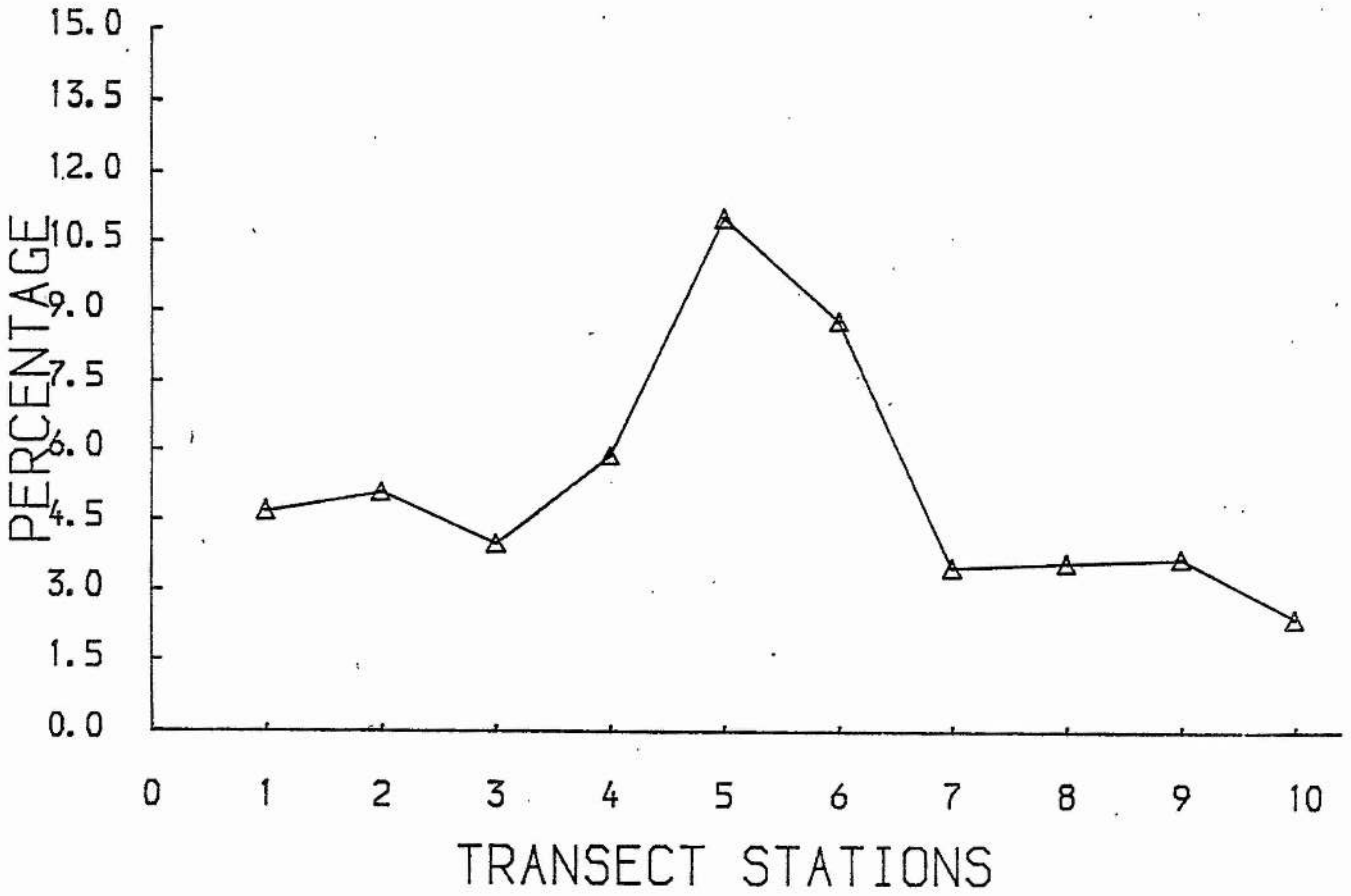

GRAPHIC SKEWNESS
SKEWNESS
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
0
1
2
3
4
5
6
7
8
9
10
TRANSECT STATIONS
AUGUST 78 w/ CaCO3
AUGUST 78 w/o CaCO3
APRIL 80
APRIL 80 S1
APRIL 80 S2

Figure 4-5

Percentage carbonate by weight for sediments collected along the transect at Tentsmuir Beach. See Appendix I for details of sample collection and treatment and Appendix Figure I for locations of sampling sites.

PERCENT CARBONATE BY WEIGHT



△ AUGUST 1978

Figure 4-6

Ripple bedding diagram modified from Reineck and Singh (1975).

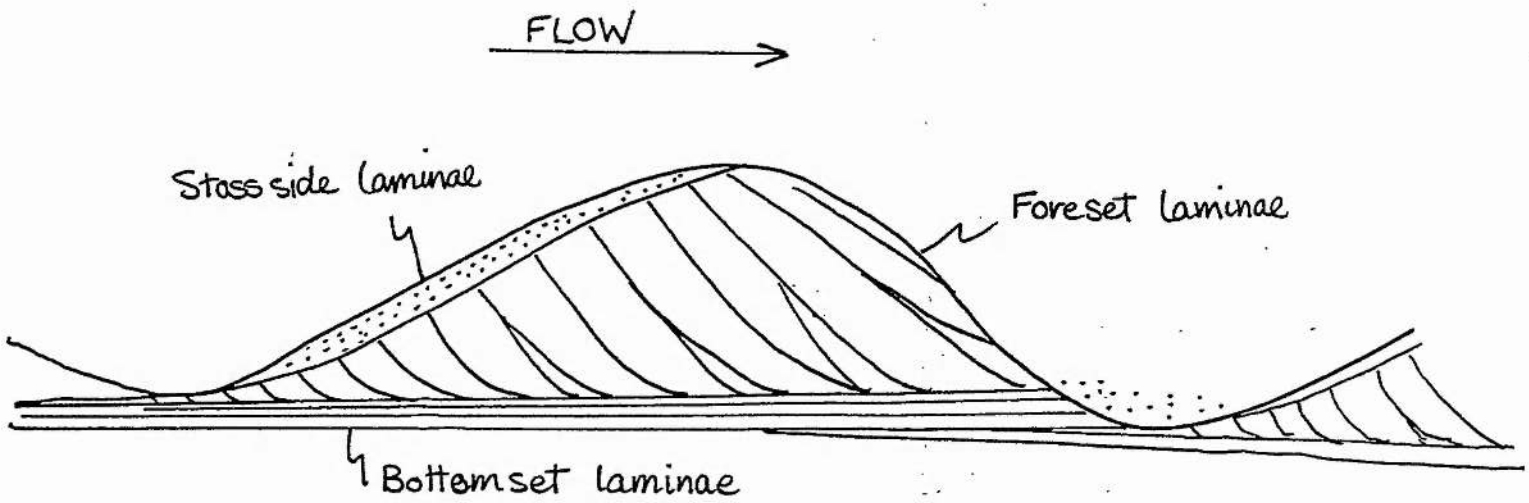

FLOW
Stoss side laminae
Foreset laminae
Bottomset laminae

Figure 4-7

Resin peel from crest of a megaripple.

See text page 58 for explanation.

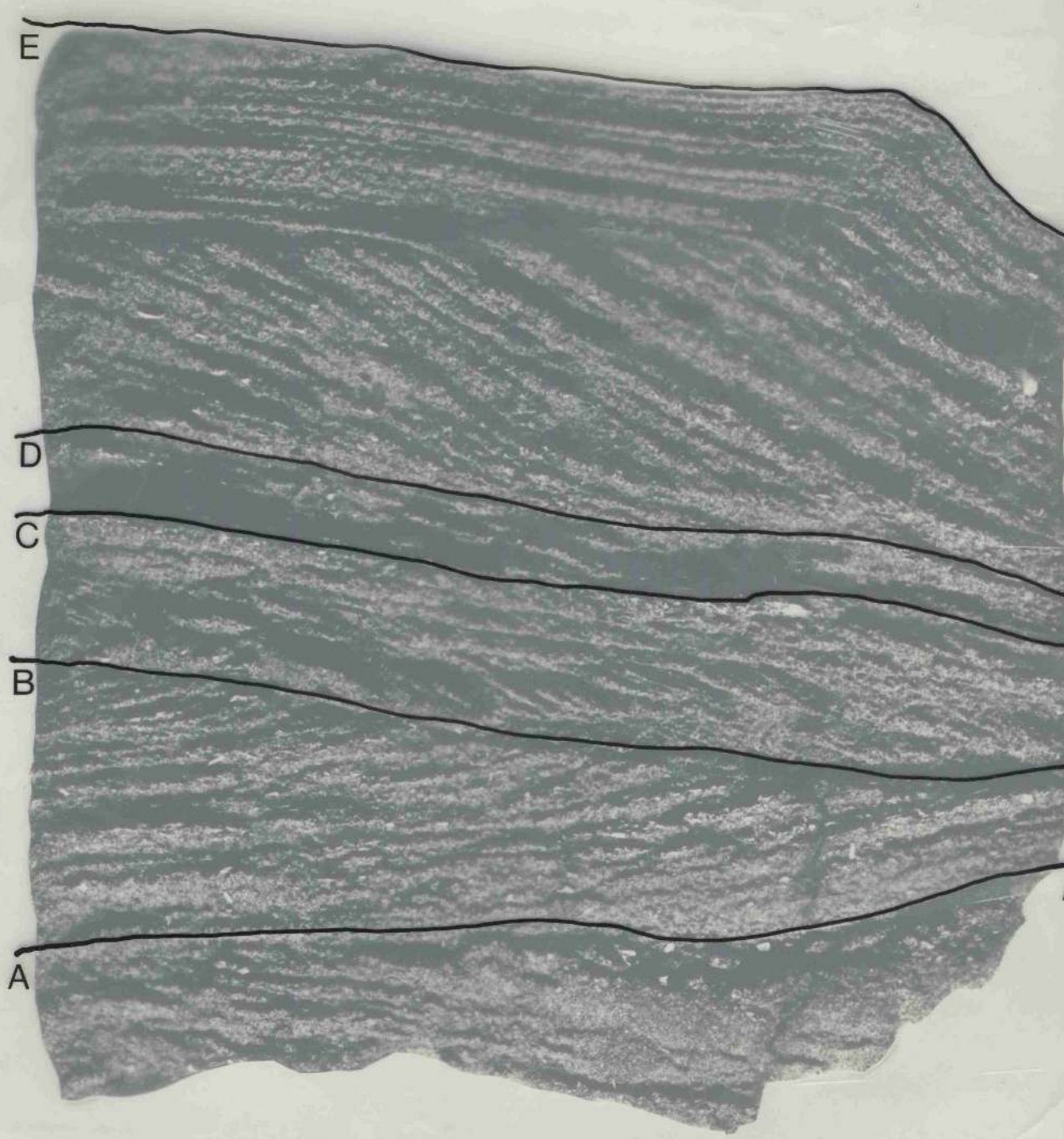

E
D
C
B
A
2 cm

Figure 4-8

Resin peel of boxcore from islet.

See text, page 62 for explanation.


5 cm
C
D
T
Sh
S
br
L
L
bl
S
Sh
B
J
S
Sh
J
U
L
A
S
Sh
L

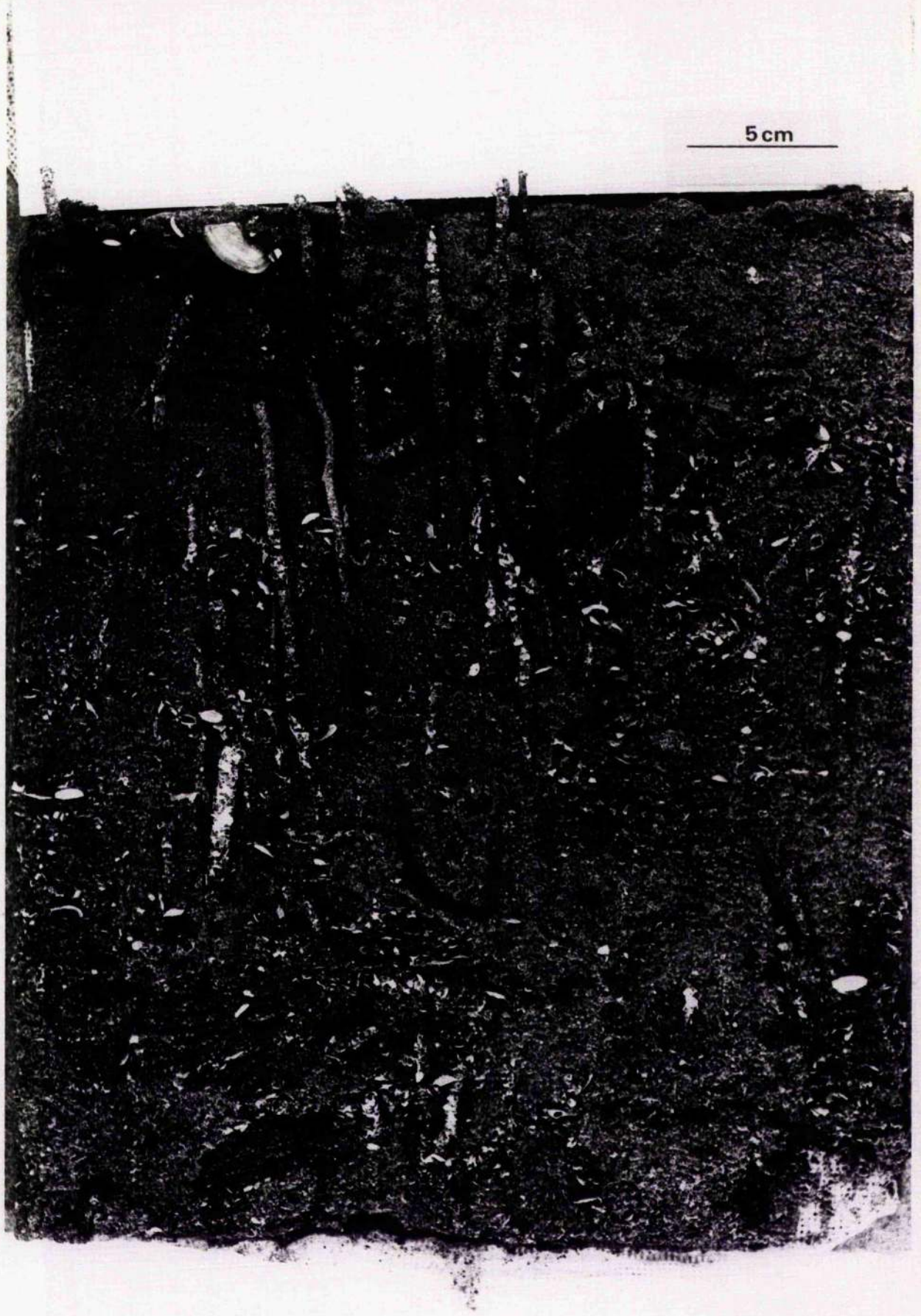

5 cm

Figure 4-9

Washed boxcore from algal-*Lanice* mound collected in July 1978.

This was prepared by carefully washing the loose sediment from a boxcore and placing the tubes and algae on botany paper. See text, page 66 for explanation.

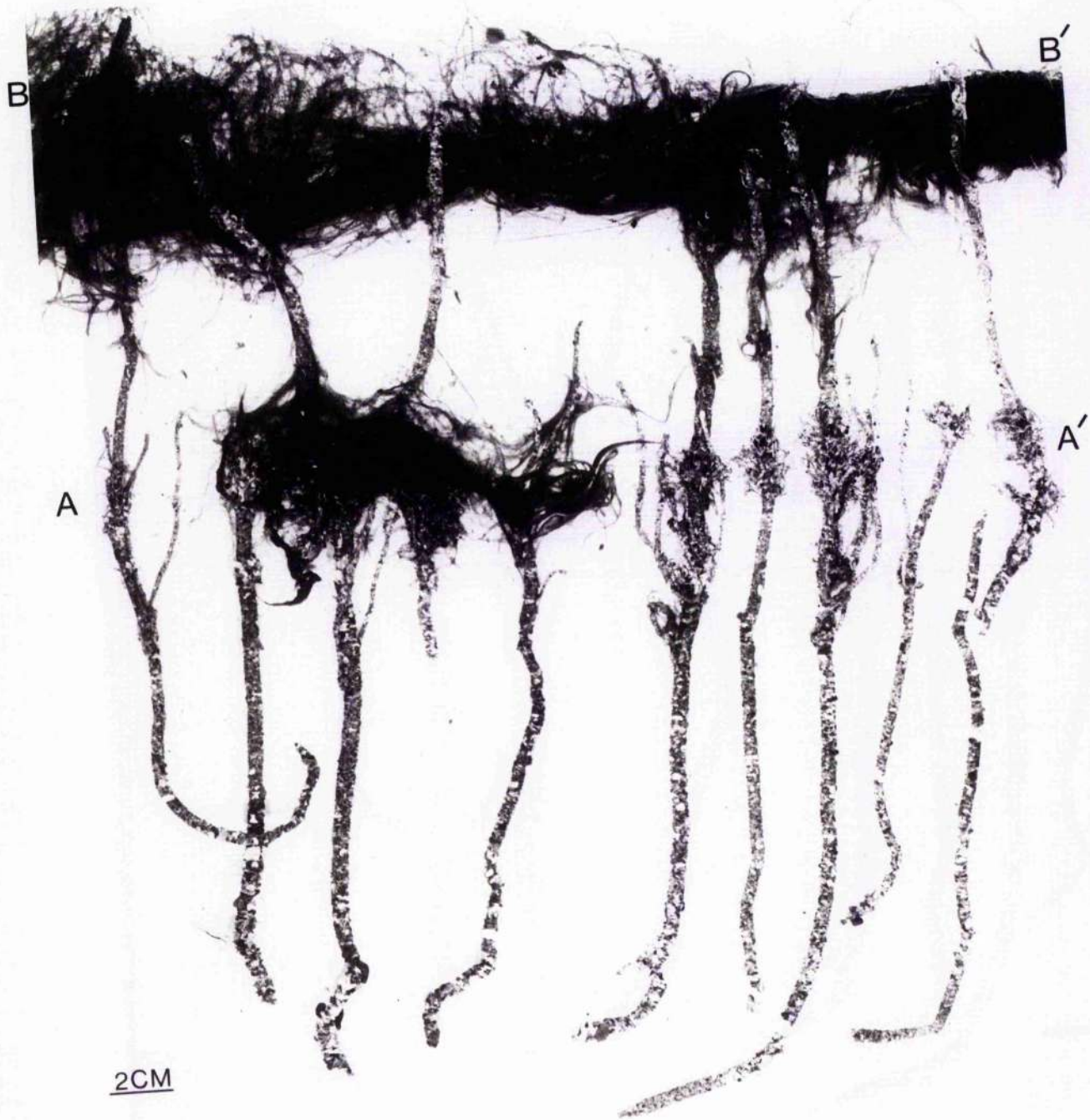

B
B′
A
A′
2CM

Figure 4-10

Detail from washed core in Fig 4-9

See text, page 65 for explanation. This detail has been enlarged 1.5 times life size.


T
F
J

5 Chapter 5 Ecological analysis

5.1 Infaunal community

The frequencies of occurrence and the abundances of the major macroinfaunal species of the Lanice tidal channel sub-environment are summarised in Table 5-1. The infaunal community abundance is numerically dominated by the tube-building polychaete Lanice conchilega. Within this community, two species assemblages were delineated on the basis of occurrence and abundance. One assemblage is here termed the Lanice conchilega association and occurred in aggregated patches positively associated with the density of the tubes of Lanice. The Lanice conchilega association was characterised by high densities of Lanice and the presence of cryptic, scavenging polychaetes (Eumida sanguinea, Anaitides maculata, and Harmothoë lunulata). The other assemblage is here termed the shallow sand association and was found generally distributed, and not strongly associated with Lanice tube density. This shallow sand association is comparable to the boreal shallow sand association of Jones (1950) and the Tellina community of Spärck (1935); it was characterised by deposit-feeding polychaetes, suspension-feeding bivalves and amphipods, all adapted to rapid burrowing in exposed sand habitats (Nephtys[1] cirrosa, Ophelia limacina, Tellina tenuis, Donax vittatus, Bathyporeia pelagica; the above species will hereafter be referred to by genus, see Appendix III for details of identification).

1. Nephtys spelling after Hartmann-Schröder (1971).

Ollivier (1969), Eagle (1975) and Buhr (1979) have described species associations dominated by Lanice conchilega. The shallow sand association has been described from various Scottish beaches (West Sands, St. Andrews, Stephen 1929; Kames Bay, Watkin 1942; Firemore Bay, McIntyre and Eleftheriou 1968; West Coast, Eleftheriou and Nicholson 1975). Eleftheriou and others surveyed the macrofauna on two transects at Tentsmuir in September 1978 and Dr. Eleftheriou has kindly provided some of their preliminary results which will be considered below (referred to as Eleftheriou pers. comm.).

Lanice conchilega is widely distributed in European waters (Atlantic Coast: Denmark, Blegvad 1914; Scotland, Solway Firth, Perkins 1974; England, Liverpool Bay, Eagle 1975; Towy Estuary, Howells 1964; Tamar Estuary, Spooner and Moore 1940; France, Roscoff, Ruillier 1959, Amoureux 1960; Dinard, Ollivier 1969; Gouville-sur-mer Manche, Hommeril 1962. North Sea: Germany, Caspers 1938, Ziegelmeier 1952, 1963, Reineck et al. 1968, Dörjes et al. 1969, Reimann-Zürneck 1969, Stripp 1969, Hauser 1973, Rachor and Gerlach 1978, Buhr 1976, 1979; Netherlands, Beukema 1976; Scotland, McIntosh 1875, Cunningham and Ramage 1888, McIntyre 1958; England, Alexander et al. 1935).

Lanice is noted for: its distinctive vertical tube (Wohlenberg 1937, Seilacher 1951, Zeigelmeier 1952); its aggregated habit (Zeigelmeier 1952, Beukema 1976, Buhr and Winter 1977, Buhr 1979); its preference for well-sorted sands and strong currents (Ziegelmeier 1952, 1969, Amoureux 1960, Hommeril 1962, Howells 1964, Ollivier 1969, Buhr and Winter 1977); and its distribution from low-water to 50 m (Spooner and Moore 1940;

Reineck et al. 1968, Perkins 1974, Buhr and Winter 1977, Rachor and Gerlach 1978). These attributes, combined with its large size (tube 1-7 mm diameter, 1-50 cm long; body tissue 1-35 mg dry weight Buhr and Winter 1977, this study) are here considered to be the primary features which contribute to the character of the distinct assemblages dominated by Lanice conchilega.

Infaunal samples were classified according to the division distribution observed at the time of collection (see Chapter 3). The divisions have been grouped into classes of tube density: high, >1000 tubes m^{-2}; moderate, <1000, >100 tubes m^{-2}; low, <100 tubes m^{-2}. The high tube density class included the algal-Lanice mound, Lanice flat, and islet divisions; moderate tube density class included the small ripple field and beach face divisions; low tube density class included the pool, drainage channel and megaripple field divisions (see Table 3-1). These three classes are compared in Table 5-2 with Lanice dominated associations described by Ollivier (1969), Eagle (1975) and Buhr (1979), and in Table 5-3 with Tellina dominated associations described by Stephen (1929) and McIntyre and Eleftheriou (1968). The basis of comparison in these tables is the frequencies of occurrence and average densities of infaunal species common to at least two of the associations.

The only genus in both tables is Nephtys, this suggests that Nephtys is not strongly associated with Lanice. This conclusion is supported by the lack of association between Nephtys density and Lanice density and Lanice tube density (Table 5-2, Lanice density and observed tube density were not synonomous; see page 73 for discussion). Tellina was not present in any of the other Lanice associations and also did not show a strong

association with Lanice tube density (Table 5-3). Ophelia was not present in any of the other associations which suggests that it is not strongly associated with either Lanice or Tellina. Donax was present in Stephen's association (without Lanice) but was not present in any other Lanice association. Its density was not strongly associated with Tellina density but clearly Donax can inhabit similar substrata. The genera described above (Nephtys, Tellina, Ophelia and Donax) were assigned to a shallow-sand association not strongly associated with Lanice but present in the Lanice tidal channel sub-environment.

Eumida was present in all of the Lanice associations and its density was associated with Lanice density and Lanice tube density (Table 5-2). Anaitides was also present in all of the Lanice associations but its density was not as clearly associated with Lanice density or Lanice tube density.

Harmothoë was present in three of the four Lanice associations and was apparently replaced by another polynoid Phloë minuta in the other (Eagle 1975). Harmothoë density was not clearly associated with Lanice density, but was with Lanice tube density. Scoloplos armiger (an Orbiniid polychaete) was present in all of the Lanice associations but was not abundant at Tentsmuir. Venerid bivalves were present in three of the four Lanice associations and were perhaps replaced by the Scrobiculariid bivalve Abra alba in the two sublittoral Lanice associations (Eagle 1975 and Buhr 1979, Table 5-2). Venerid bivalve density was not associated with Lanice density and they were not common or abundant at Tentsmuir. The genera described above that were common at Tentsmuir (Eumida, Anaitides and Harmothoë) were assigned to the Lanice conchilega association present in

the Lanice tidal channel sub-environment.

5.1.1 Distribution of macrofauna

The distribution of species and environmental divisions at the Tentsmuir study area from May to September 1978 is illustrated in Figure 5-1. The easily disturbed habitats (megaripple field, drainage channel, pool) were observed to contain small numbers of large, suspension-feeding bivalves (Ensis siliqua, Spisula solida, Cerastoderma edule) although they rarely were found in the core survey (see Appendix Table I). These species were found throughout the study area but their greatest densities occurred in the disturbed habitats.

Several members of the large, vagile (migrant) invertebrate epifauna were observed, and occasionally found in core samples. Of these, mysid shrimps (Mysidae) and common shrimps (Crangon crangon) were observed in pools, particularly from May-September. The shore crab, Carcinus maenas, was commonly found sheltering in algal masses, scour pits, and at the edge of Lanice flats and algal-Lanice mounds. Juvenile C. maenas were occasionally found in large numbers in core samples (22 in an algal-Lanice mound adjacent to an eider browsing trace from March 1979). Young C. maenas were often found sheltering in the hollow poles used to mark the stations on the transect.

Juvenile plaice (PLeuronectes platessa) and dabs (Limanda limanda) were observed in large numbers in pools from April until late August, but were not taken in any cores. The sand-eel (Ammodytes tobianus) was often found just beneath the sand surface in the megaripple fields, pools and small ripple fields throughout the year and occasionally was found in cores.

Amphipods (Haustoridae, Gammaridae and Atylidae) were generally distributed throughout the study area but were excluded from faunal counts in this study because of suspected errors in sampling. Eleftheriou (pers. comm.) listed five species of amphipods (Bathyporeia guillamsonia, B. elegans, Pontocrates arenarius, Atylus swammerdami, and Gammarus locusta) and two cumaceans (Cumopsis goodsiri, Psuedocuma gilsoni) from a station within the study area in September 1978.

Spat (juvenile bivalves) of the mussel (Mytilus edulis) were found in large numbers in the study area from March until October in 1979. No adults were observed in the study area but one adult was found in a Lanice flat in the middle of the tidal channel. The spatfall was occasionally dense enough to make the exposed tops of the Lanice tubes appear black.

Three polychaete species were commonly found in tubes occupied by Lanice conchilega: Eumida sanguinea, Harmothoë lunulata and Anaitides maculata. Eagle (1975) reported Eumida (as Eulalia sanguinea) living in empty Lanice tubes. Buhr (1979) also found Eumida (he did not differentiate between Eumida (Pirakia) punctifera and Eumida sanguinea) in empty Lanice tubes, and remarked that lab investigations indicated that

Eumida fed on the tips of the tentacles and abdomen of Lanice. Buhr (1979) reported Harmothoë imbricata and H. lunulata from Lanice tubes.

Three species were occasionally found in empty Lanice tubes: two polychaetes, Nereis pelagica, and Scoloplos armiger; and one nemertine, Amphiporus lactifloreus.

Lanice conchilega can build numerous tubes during its lifetime (1-5 years), if these tubes are not disturbed they can remain intact in the substratum for considerable periods of time (Ziegelmeier 1952, 1969). These empty tubes will rapidly fill with sediment if not cleared periodically by an active worm. The observed density of tubes on the surface may, therefore, give a misleading impression of the actual density of live Lanice within the tubes. Tube density is strongly associated with actual live animal density (Table 5-2), but Buhr (1979) reported an average ratio of 1.75 occupied tubes: 1 unoccupied tube (range 10:1 - 0.05:1) from 28 subtidal stations. Five samples from Tentsmuir had a ratio of 1.18 tube tops observed on the surface to 1 worm counted in the sample (range 1:1-1.38:1).

Occupied and unoccupied tubes increase the physical complexity (structural heterogeneity) of the well-sorted sediment and can provide refugia for cryptic species and perhaps even substrata for attachment of meiofauna and algae (Eleftheriou pers. comm, Myers 1972 and Brenchley 1976). Increased structural heterogeneity has been shown to increase species abundance and biomass (Woodin 1976, 1978, Heck 1979, Wilson 1979). For these reasons it is important to examine the relationship between the structural character of the stations (divisions)

and the infaunal abundance and biomass.

The abundance of all infaunal species decreased seawards along the transect (Figure 5-2) and although dominated by Lanice conchilega retained a consistent pattern when plotted without Lanice (Figure 5-3).

Stations 3, 7, 8, 9, & 10 with low abundance values and Station 5 with intermediate values had the smallest variations in total abundance during the sampling period. The stations with peak values (2, 4, & 6) had the greatest variation. These results are consistent with the transition frequencies observed between environmental divisions at the same stations (Figures 3-13, 3-14). Stations 3, 7, 8, 9, & 10 remained within the low tube density, high disturbance class of divisions and 5, although temporarily buried by ripples, remained a stable area. Stations 2, 4, & 6, however, all experienced periods of dense settlement or erosion. The variation in total abundance was primarily due to large fluctuations in the number of Lanice encountered in the samples (compare Figure 5-2 with Figure 5-3). Lanice had a highly contagious distribution (aggregated) except at very high tube densities when it often had an apparent regular distribution (evenly spaced) within patches (Figure 5-25). Removal of Lanice abundance from the total demonstrated that the greatest variation in abundance was in the marginal areas (Stations 2 and 6, Figure 5-2, 5-3).

The variation in species richness was less clear (species richness taken here to be the simplest measure: number of species in each sample; this represents areal species richness or species density, Hurlbert 1971), the number of species declined seawards but the greatest variation was at Station 10 due to an unusually high number of species in the May 1978

sample (Figure 5-4). The highest numbers of species generally coincided with the highest abundances but the trend of high values to landward and low values to seaward appears to have overwhelmed the fluctuations in abundance.

The total infaunal abundance within the megaripple field (7, 8, 9, & 10) was an order of magnitude lower than within the landward areas (Figure 5-2). If we examine the figures without Lanice abundance (Figure 5-3), the decrease is not so dramatic and may reflect an increase in tidal current disturbance towards the tidal channel. This suggestion is supported by the gradual decrease in species richness (Figure 5-4). The sharp drop in the abundance of Lanice is also reflected in the truncated distribution of Lanice tubes described in Chapter 3 (see Figure 3-1).

5.1.2 Biomass

The distribution of biomass (ash-free dry weight of soft tissues, Figure 5-5) was closely related to the distribution of the dominant species, Lanice conchilega (Figure 5-7). Biomass values along the transect are only available for May 1978 (see Appendix II) and provided a means of evaluating the levels at the beginning of the survey.

In May 1978 Station 5 was an established Lanice flat, a surviving remnant from the previous summer and populated by relatively old worms with large tubes. Stations 1, 2, 4, & 6, however, were areas of new settlement which formed algal-Lanice mounds and were populated by relatively young

worms. These field observations are supported by a comparison of the biomass values (Figure 5-5) and the abundance values (Figure 5-6) for each station. Station 5 had a higher biomass value (5.03 g) relative to the abundance value (157) than Stations 1, 2, 4, or 6 (5.00:196, 3.49:167, 3.48:101, 3.21:154 respectively). This relationship between age class of Lanice and biomass can also be seen in the biomass values from two Lanice flat samples from July 1978 (HD1, HD2 in Appendix Table II). In these samples the Lanice were sorted into adult and juvenile classes (juveniles: tube diameters < 2mm) and weighed separately. Despite the numerical dominance of juveniles in these samples (HD1: 88.66%, HD2: 68.32%) the ash-free dry weight of the adults constituted > 80% of the total Lanice dry weight.

The biomass of polychaetes other than Lanice generally followed the distribution of Lanice biomass (low values at Stations 3, 7, 8, 9, 10 and high values at Stations 1, 2, 4, 5, 6) but had anomalously low values at Station 2. The sample from Station 2 did not have any large polychaetes (Nereis diversicolor, Nephtys caeca or Anaitides groenlandica) or high numbers of Ophelia limacina (Appendix Table III).

The biomass of bivalves also generally followed the distribution of Lanice biomass but had a relatively low value at Station 1 and a very high value at Station 10. The sample from Station 1 lacked any large bivalves (Spisula solida, Cerastoderma edule, Ensis siliqua, Donax vittatus) whilst Station 10 was located within the area dominated by Spisula solida (see Figure 3-10) and this sample contained three large Spisula.

The Lanice biomass values for the samples from the Lanice flats (HD1, HD2) compare closely with those reported by Buhr (1979) from a subtidal Lanice-dominated association. The average dry weight per individual in Buhr's largest size class ranged from 56-216 mg (average 134 mg) and the average weight in his smallest size class ranged from 0.7-10.9 mg (average 4.27). The average dry weights per individual in the adult class from samples HD1 and HD2 were 113 mg and 94 mg respectively. The values for the juvenile class were 2.7 mg and 5.0 mg. The overall average for all Lanice in all nine samples with Lanice was 34.21 mg individual $^{-1}$.

Total biomass values for these samples are very high. The average total biomass from samples with Lanice was 61.28 g m^{-2} (range 21.5-150.87). Even the total biomass excluding Lanice was high, for these samples the average was 19.13 g m^{-2} (range 8.78-28.15). The average total biomass in the samples without Lanice present was 8.39 g m^{-2} (range 0.76-30.5). All of these values can be taken to be summer biomass levels, the winter biomass is expected to be much lower (Beukema 1976). Even taken as an upper range of an annual figure the biomass recorded at Tentsmuir exceeds most published figures for intertidal sand flats and beaches in North European waters.

McIntyre (1958) found 4.19 g m^{-2} as an average dry weight in fine sand at 10-20 m depth in St. Andrews Bay. McIntyre (1970) and Eleftheriou and Nicholson (1975) classified some Scottish beaches as sheltered, semi-exposed, and exposed, and reported ranges of 2.30-31.04 g m^{-2}, 0.86-3.14 g m^{-2}, and 0.16-0.62 g m^{-2} (respectively). The biomass values excluding Lanice would fall within the range of sheltered beaches, whilst

the biomass values for samples with no Lanice present would fall within the semi-exposed range.

Beukema (1976) reviewed tidal flat biomass data and reported a range in annual average ash-free dry weight from North Sea tidal flats of 24-45 g m^{-2}. Beukema (1976) suggested that a reasonable estimate of the average biomass of macroinfauna of the entire Dutch Wadden Sea would be close to 20 g m^{-2}.

McIntyre (1978) reviewed the available benthic biomass data for the entire North Sea but apart from high wet weight biomass values from Pygospio/Cerastoderma (as Cardium) and Scrobicularia/Mya flats in the Wadden Sea (from Linke 1939) he reported no dry weight values, intertidal or subtidal, equivalent to those reported here and by Buhr (1979). Eleftheriou (pers. comm.) found wet weight values of 230.28 g m^{-2} in a Lanice dominated sample from Tentsmuir in September 1978.

Birkett (1954) reported a maximum dry weight value of 41 g m^{-2} for a dense Mactra (Spisula) patch on the Dogger Bank and Stripp and Gerlach (1969) found a mean wet weight of 16 g m^{-2} in a subtidal Tellina tenuis community in the German Bight. These values are equivalent to the values in the samples with no Lanice present.

5.1.3 Seasonal variation

MAY 1978

By May 1978, settlement and growth of Lanice juveniles had begun and algal sporlings were evident on the surface. These events initiated a period of rapid accretion of algal-Lanice mounds and further settlement of Lanice and algae. Eider disturbance had also begun (recorded from March 1978) and holes were evident throughout the Lanice occupied parts of the study area.

Station 5 was a dense Lanice flat and Stations 1, 2, 4, & 6 were areas of new settlement of both Lanice and algae. The abundance values over the whole transect show less variation than at any other sampling time (range 11-197 individuals, Figure 5-6). This is perhaps because the transect had been eroded during the previous winter and settlement had only just begun. Samples collected in May from other dense patches had higher total abundances than any of the transect samples (MS=233, PF=281; see Appendix Figure I and Appendix Table I for location and distribution of samples). These patches to the north and south of the transect had survived the winter relatively intact.

Lanice was most abundant at Stations 5 (Lanice flat) and 1 (algal-Lanice mound), but relatively low at the other algal-Lanice mound Stations (2, 4 & 6; Figure 5-7). The Lanice abundance at Station 3 although low (28) was higher than at any subsequent sampling period, an indication that the initial settlement was unsuccessful at this station. The formation of an enclosed pool at Station 3 was evident in May 1978, and

due to the higher relief of adjacent algal-Lanice mounds. The density of Lanice at Station 3 apparently was not sufficient to form algal-Lanice mounds at this time and the population declined as is discussed in sections 5.2 and 5.3. The lowest Lanice abundances in May 1978 were recorded from Stations 7-10, as was the case throughout the rest of the year.

Tellina abundance was higher at Station 6 than at any other sampling period. This disrupted the usual pattern of a peak at 2 and gradual decline to 6. The high abundance in the sample would appear to have been an isolated dense patch of Tellina which was not sampled subsequently. Combined Nephtys and Ophelia abundance was reasonably constant along the transect with a low value from the drainage channel at Station 7. Nephtys was higher at Stations 8, 9, & 10 in May than at any other sampling period. Eumida, Harmothoë and Anaitides, taken together, were also evenly distributed from Stations 1-6, declined in the drainage channel and in megaripple Stations (7-10).

Station 10 had a higher abundance in May than at any other sampling period. This was due to a dense population of Spisula solida (3-4 year class) observed along the low water margin of the tidal channel. This population was not encountered in any subsequent samples at Station 10 but the population was observed at other times when Spisula came to the surface 10-20 m south (Figure 3-10).

AUGUST 1978

Lanice settlement and algal growth accelerated between May and August 1978 and the topography of the study area became well-established (see Figures 3-1 and 3-4 from September 1978). Eider feeding activity declined from May, and from July no eiders were observed. Physical disturbance during this period was at a minimum, with no storms affecting the beach (Figure 2-4, profiles 26 July and 17 August). Juvenile plaice (Pleuronectes platessa) and dabs (Limanda limanda) were abundant in the pools and the embayment. Dense patches of juvenile Lanice tubes were observed in July (see Figure 5-24b). Two samples from a high density area (see Appendix Figure I for location) contained very high numbers of juveniles (HD1: 33 adults, 258 juveniles. HD2: 102 adults, 220 juveniles; see Appendix Table II). The washed core described in Chapter 4 (Section 4.2.2 and Figures 4-9, 4-10) also recorded dense clusters of juveniles in July.

Stations 4 and 6 developed into Lanice flats in August but only Station 4 showed an increase in total abundance (Figure 5-8) or an appreciable increase in Lanice abundance (Figure 5-9). Station 6 dropped in Lanice abundance and the abundance without Lanice, whereas Stations 1 and 2 (both still algal-Lanice mounds) increased in Lanice abundance and dropped slightly in the abundance of all other species (Figure 5-8). Station 3 was a very distinct pool in August and the abundances of all species apart from Tellina and Ophelia declined. The drop in Lanice abundance at this station was dramatic considering the increase at adjacent stations (Figure 5-9).

Tellina was more abundant at Station 4 than during any other sampling period, this may have been due to sampling a discrete dense patch as the other stations decreased slightly. The abundances of Eumida and Anaitides were low at all stations but Harmothoë was unusually abundant at Stations 1, 4, & 5 (Figure 5-9). Nephtys abundance was generally low in August with normal values at Stations 2, 5, & 7, Ophelia was also high at 7 and unusually high at 4.

OCTOBER 1978

By October 1978 two substantial storm periods had occurred, one at the beginning of September and one at the beginning of October (see Figure 2-4, profiles 20 September and 7 October). The red and brown algae began dying in mid-September and the green algae at the beginning of October. The first storm period (6 September) removed some groups of algal-Lanice mounds and buried many others. The disturbed tubes and piles of algae attracted wading birds and gulls (35 gulls, 2 terns, 17 oystercatchers on 8 September). By the following spring tides (16-20 September) the algae and worms had re-established a dense cover, although mounds that had been completely eroded were now small ripple fields (see Figure 3-1, taken on 19 September). Shore crabs (Carcinus maenas) were abundant at this time, 15 moults were found in one 10 m^2 count on 4 September and one large crab (carapace width 10 cm) was found near Station 6 on 18 September.

The second storm occurred on 1 October and altered the runnel profile sufficiently to move the runoff channel to a position emptying onto the study area. This runoff carried bedload from the beach and deposited it on the study area. The death of most of the algal cover before this storm resulted in extensive erosion during the storm (see Figure 3-11a).

The area of the transect was not greatly affected by erosion at this time, algal-Lanice mounds at Stations 1 and 2 became islets and the margins of the Lanice flats were eroded but the abundance of Lanice in these areas was higher than in August (Figure 5-10). Stations 2 and 6 had the highest Lanice abundances and were the most eroded areas. The samples were taken within the remaining islets and the high density may have aided their resistance to erosion. Stations 7 and 9 were not sampled in October as they were submerged areas of extremely soft sand and the can-core technique failed to collect intact samples. Station 8 was also very soft and numerous sand eels (Ammodytes tobianus) were observed just below the surface (two were collected in the 0.08 m^2 sample). Station 10 was much firmer sand, and Spisula solida was found in the sample.

Station 3 was still located in a well-defined pool although many of the surrounding mounds had been reduced in size. Lanice abundance was very low at Station 3 but large specimens of Nephtys caeca and Cerastoderma edule were found in the sample. Stations 4 and 5 remained as stable Lanice flats but had lower Lanice abundance than the islets (Figure 5-10).

Tellina abundance in October reflected the general distribution of Tellina; low at neap low water, peak just below neap low water and gradual decline to a minimum at spring low water. Nephtys abundance was at its highest level (20) of any of the samples at Station 1, but the rest of the stations had normal abundances. Ophelia abundance also had an all-time peak (13) at Station 4, a Lanice flat, but only two Ophelia were found in the sample from Station 5, also a Lanice flat. Eumida and Anaitides both had abundance peaks at Station 2 and Eumida also had high abundance at Station 1 (Figure 5-11).

The combination of relatively high abundances of Tellina, Eumida, and Anaitides at Station 2 caused this station to have the highest total abundance in October despite Station 6 having the highest Lanice abundance of any of the transect samples. The sampling in October recorded the highest abundances for many species and the second and fourth highest total abundances of the transect survey. This appeared to represent the culmination of the settlement and growth of infaunal species during the summer as abundance distribution patterns remained similar but higher than those of August.

MARCH 1979

Between October 1978 and March 1979 the study area was subjected to a series of strong easterly gales (8-9 December, 23-24 January) which flattened the beach profile and eroded the mounds of tubes (see Figure 2-5, profile 28 January, 27 March). On the 27 and 28 of January the beach was frozen during spring tides at night and during the day. The distribution

of field divisions was mapped at this time and is shown in Figure 3-6. Lanice tube tops were generally ragged ends of tubes, very few tubes were observed to have completed fringes. The tubes were also mainly small (2-4 mm diameter) indicating either: little growth during the winter; late settlement; or death of the older, larger worms and burial or erosion of their tubes. As the beach was flattened, the slope between the top of the megaripple bar and the tidal channel also flattened and very few Spisula were observed on the surface. In late March (27th) Eiders were again observed feeding and producing browsing traces. The beach was still flat and an easterly gale hit the beach on 29 March (during the sampling period).

Despite the severity of the winter and the extensive modification of the study area, high abundances were recorded following a similar pattern to August and October 1978. Stations 1, 5, and 6 were clearly affected but Stations 2 and 4 retained the species abundances of the summer (Figure 5-12). Station 1 was part of the sloping beach face in March 1979 and low species abundances were recorded, Eumida, Harmothoë and Anaitides were absent and Tellina and Lanice abundances dropped, only Nephtys and Ophelia seemed to be unaffected (Figure 5-13). The total abundance, total without Lanice and species richness were all lower in March at Station 1 than at any other sampling period (Figures 5-2, 5-3, 5-4).

Stations 5 and 6 dropped down to pre-May 1978 levels of Lanice abundance (Figure 5-16) as the islets were eroded to small ripple fields. The changes in abundance of the other species (apart from Eumida) were not clearly related to this erosion event (compare Figures 5-11 and 5-13). Eumida was absent from both stations and Harmothoë was absent from Station

5, but Harmothoë abundance increased at Station 6 (Figures 5-18 and 5-19). Anaitides abundance remained high or increased at both stations (Figure 5-20). Nephtys and Ophelia increased at Station 5 but dropped in abundance at Station 6, whereas Tellina abundance dropped at Station 5 and remained the same at Station 6. Despite these conflicting fluctuations the overall trend was a drop in total abundance without Lanice at both Stations 5 and 6 (compare Figures 5-10 and 5-12).

Stations 2 and 4 had high numbers of Eumida and the second and third highest abundances of Lanice, (Figure 5-16, 5-18). Station 2 had the highest abundance of Tellina and Anaitides of any sample (Figure 5-15, 5-20).

Ophelia abundance was relatively low throughout the transect (Figure 5-17) with the highest values at Stations 1 and 5 (the two most disturbed stations). Nephtys abundance was relatively high throughout the transect but surprisingly absent from Station 9.

Station 3 was still a pool although very shallow and again no Lanice were recorded from this station. Nephtys and Tellina were not low but Ophelia was and Eumida, Harmothoë and Anaitides were absent (Figure 5-13).

The high abundances recorded in October 1978 seemed to persist through the winter at stations that still retained high numbers of Lanice. The low temperatures and strong wave activity did not seem to affect the species discussed here. In October most of the epifauna and algae had disappeared and was only just beginning to reappear in March 1979. Other samples in March recorded very high numbers of mussel spat (Mytilus edulis) and

clearly larval settlement had begun in earnest at this time (LTC1: 150 spat, LTC2: 35 spat; Appendix Table I).

5.1.4 Common species

The distributions of the seven most common species over all sampling periods are presented in Figures 5-14 to 5-20. They will be discussed briefly with some notes on the ecology of each species.

Nephtys cirrosa

Nephtys cirrosa was the most common species in the area sampled by the transect survey (Table 5-1). No consistent pattern is apparent for its distribution spatially or temporally (Figure 5-14). Unlike the other common species Nephtys abundance did not decline precipitously in the megaripple field (Stations 7-10). Nephtys abundance did not seem to be affected by the presence of high densities of Lanice or Lanice tubes (Table 5-2).

The average density of Nephtys at Tentsmuir was 105 individuals m^{-2}. Clark and Haderlie (1950), Clark et al. (1962) and Amoureux (1968) reported N. cirrosa from clean sandy beaches. Wolff (1973) reported it from well-sorted medium sand with a vertical distribution from the upper intertidal to at least 35m depth. McIntyre and Eleftheriou (1968) recorded N. cirrosa as the most widely distributed infaunal species at Firemore Bay.

N. cirrosa is widely reported as a predator, feeding on small invertebrates, but no information is available on specific prey (Schäfer 1972, Wolff 1973, Faushald and Jumars 1979), although Clark (1962) reported mainly polychaete remains from N. cirrosa. Nephtys spp. build poorly agglutinated mucus burrows and can be considered free-living burrowers (Schäfer 1972, Ronan 1978, Fauchald and Jumars 1979). These conclusions are consistent with the ubiquitous distribution of Nephtys along the transect, Nephtys burrows through well-sorted clean sand and presumably ingests a wide variety of small infaunal animals. Nephtys spp. have large eversible pharynges (for burrowing and feeding) and are strong, muscular burrowers (Clark 1962, Schäfer 1972, Fauchald and Jumars 1979), this should enable them to successfully withstand the rigours of life in a megaripple field, as they apparently do at Tentsmuir. There is no reason to suppose that the areas occupied by dense aggregations of Lanice tubes are any less attractive as a habitat for Nephtys, as these areas had higher abundances of a variety of small invertebrates, and on one occasion (March 1980) N. cirrosa was found in an unoccupied Lanice tube. The density of N. cirrosa at Tentsmuir was comparable to the maximum density previously reported ($100m^{-2}$, McIntyre and Eleftheriou 1968) and is within the range of densities ($100-150m^{-2}$) considered by Clark (1962) to be the normal upper limit for Nephtys spp.

Tellina tenuis

Tellina tenuis was the second most common species in the area sampled by the transect survey (Table 5-1). Tellina abundance rose from Station 1 to a peak at Station 2 and declined gradually to very low values from Stations 7-10 (Figure 5-15). The low abundance corresponded to the drainage channel and megaripple field, but was not observed in the pool. Tellina abundance does not seem to be affected by the presence of high densities of Lanice or Lanice tubes (compare Figures 5-15, 5-16); the low abundance values in Table 5-3 would appear to confirm this. The average density of Tellina at Tentsmuir was 483 individuals m^{-2}.

Clark and Milne (1955), McIntyre and Eleftheriou (1968), McIntyre (1970), Tebble (1976) and McKay and Smith (1979) reported T. tenuis from Scottish beaches, they all agreed that T. tenuis was common in clean sand and reached maximum densities near low water mark. T. tenuis is known to extend subtidally but it is usually replaced by greater numbers of T. fabula (Clark and Milne 1955, McIntyre and Eleftheriou 1968). Eleftheriou (pers. comm.) reported small numbers of T. fabula at Tentsmuir, and it is possible that I overlooked T. fabula in my samples, but the decline in Tellina abundance towards extreme low water and the very low abundances in the megaripple field would suggest that T. fabula was not successful in replacement of T. tenuis in this small area.

T. tenuis feeds with an extensible siphon (inhalant, separate from exhalant) on sediment particles and detritus either directly from the sediment surface or by filtering turbid water overlying the sediment/water interface (Pohlo 1969, Trevallion 1971). T. tenuis normally lies 2-12cm below the surface (deeper values at low tide) with the right valves upwards and the siphons extended to the surface (Holme 1961, Tebble 1976). It appears from this that Tellina is a potential competitor for food with Lanice (both surface particle feeders), however, there is no indication from the distribution of abundance that this had a deleterious effect on either population. It is possible that any exclusion or re-distribution effects occurred on a smaller spatial scale than the sampling of this survey. T. tenuis is a long-lived species (up to 8 years, McIntyre 1970) and the population sampled on the transect may have been in place before the Lanice settlement, if this was the case the distribution of the two species could well be entirely unrelated. No quantitative information is available on recruitment at Tentsmuir, but numerous 1 or 2 year class individuals were found in 1980, whereas the population sampled in 1978-79 appeared to comprise a single-year class (4-5).

The distribution of T. tenuis abundance along the transect can be related to large-scale physical disturbance or tide levels but does not appear to closely relate to the environment divisions (Figure 5-15). There was a departure from the trend of the distribution at the beach face and megaripple field divisions but no decline in the pool. The departure points are at extreme low water neap (Station 1 was at or above E.L.W.N.) and low water spring (Stations 7-10 only exposed at E.L.W.S.) tide levels and also correspond to changes in intensity of physical disturbance (wave

disturbance at Station 1, tidal current velocity at Station 7). Eleftheriou and Nicholson (1975) found reduced abundance of T. tenuis in exposed and semi-exposed beaches relative to sheltered beaches in Scotland. The average density at Tentsmuir is comparable to the values they found at low water in sheltered beaches for all molluscs (mainly T. tenuis, mean: 814 m^{-2}) whereas the average density in the megaripple, drainage channel and pool divisions (Table 5-4) is comparable to the values they found at low water in semi-exposed beaches (mainly T. tenuis, mean: 77 m^{-2}), they found virtually no molluscs on the exposed beaches.

Lanice conchilega

Lanice conchilega, although absent from some samples, was the numerical dominant in the infaunal survey with nearly three times the average density of T. tenuis, the next most abundant (Table 5-1). Lanice contributed over 56% of the total abundance. The environmental divisions were based, among other features, on the distribution of Lanice tubes so it is not surprising that the abundance of Lanice was closely related to the distribution of divisions. In general, Lanice abundance was very high at Stations 2 and 4, high-moderate at Stations 1, 5 and 6 and low at Stations 2, 7-10 (Figure 5-16). Exceptions to this distribution were moderate values at Stations 2 and 4 in May 1978 and very high values at Station 1 in August 1978 and Station 6 in October 1978. The average density of Lanice overall was 1390 m^{-2}. The ecology and distribution of L. conchilega are discussed in detail elsewhere in this study (Distribution: chapter 3 and Section 5.1.1; Settlement: Section 5.2; Feeding: chapter 6) and will not be treated further here.

Ophelia limacina

Ophelia limacina was as widespread in samples from Tentsmuir as Lanice (78%) but contributed only 2.7% of the total abundance (Table 5-1). There was no consistent pattern to the distribution of Ophelia, but the abundance peaked at Station 4 and was low at Station 8-10 (Figure 5-17). The initial high abundances at Stations 1 (algal-Lanice mound), 3 (pool) and 6 (Lanice flat) were reduced in later samples but only to levels equivalent to Station 2 (algal-Lanice mound). Ophelia was the only common species apart from Nephtys with a moderate abundance in any sample at station 7. Thus, although there is a superficial resemblance to the distribution of Lanice, it is not consistent and Ophelia abundance did not seem to be related to Lanice density or Lanice tube density. The average density of O. limacina at Tentsmuir was 66 individuals m^{-2}.

No clear records of the distribution of O. limacina are available as the most recent revisions of the genus are contradictory. Tebble (1972) considered the occurrence of O. limacina in British waters as doubtful and referred intertidal species to O. rathkei. This diagnosis was accepted by Clark (1960 and subsequent papers) and McIntyre and Eleftheriou (1968) and Eleftheriou (pers. comm.). Hartmann-Schröder (1971) referred Tebble's O. borealis to O. limacina and my specimens fitted her description of O. limacina (see Appendix III, notes).

The reported distribution of O. rathkei is almost exclusively intertidal (Tebble 1952) mentioned finds at 33m near the Isle of Man), and more specifically in the middle and upper intertidal. Watkin (1942) reported O. rathkei from a narrow belt just below high water neap in Kames

Bay (maximum density of 2000 m^{-2}) and Clark and Milne (1955) did not record any Ophelia species in the subtidal of Kames Bay. McIntyre and Eleftheriou (1968) recorded a maximum density of 3312 m^{-2} a little above mean low water neap in Firemore Bay and stated that it was confined to the intertidal. O. rathkei was a predominant species in the Scottish beaches surveyed by Eleftheriou and Nicholson (1975) from the "middle beach". Wolff (1973) also considered O. rathkei exclusively intertidal in the deltas of the rivers Rhine, Meuse and Scheldt and restricted to the neap tidal range.

O. borealis (= O. limacina after Hartmann-Schröder 1971) is not restricted to the intertidal but is reported from just above low water mark to a depth of 36m (Wolff 1973). This is consistent with my records of O. limacina just above low water mark and the general low water-subtidal nature of the Tentsmuir study area.

Opheliids are generally considered to be non-selective deposit feeders, although no detailed studies have been done (Fauchald and Jumars 1979). O. limacina (as O. borealis) is an active burrower in medium, well-sorted sands (Wolff 1973). Certainly the turgid body and tough epidermis of the specimens I examined would appear to be well-suited to survival in sandy beaches, unlike the very soft body and thin epidermis of a tube-dweller like L. conchilega. Ophelia abundance at Tentsmuir was low, but they were of sufficient bulk to provide a measurable portion of the biomass (average ash-free dry weight 28 mg individual $^{-1}$, Appendix Table III).

Eumida sanguinea

Eumida sanguinea was present in less than half of the infaunal samples from Tentsmuir, but in three of those samples it was present in relatively high abundances (Table 5-1). The high abundances occurred in samples from algal-Lanice mounds and Lanice flats, whereas no Eumida were present in any samples from the drainage channel or megaripple field (Figure 5-18). Eumida was uniformly distributed from Stations 1-6 in May 1978, this was before substantial settlement of Lanice (see Figure 5-16) and development of the pool-mound topography. Subsequent samples produced no Eumida from the pool (Station 3) and erratic increases in Stations 1 and 2 (algal-Lanice mounds) and 4 (Lanice flat). Eumida was associated with high Lanice abundance and high Lanice tube density (Table 5-2). This association is not surprising as Eumida was often found in occupied and unoccupied Lanice tubes. The average density of E. sanguinea at Tentsmuir was 147 individuals m^{-2}.

Wolff (1973) reported E. sanguinea in fine and muddy sand from below low water mark to 48m in the deltas of the rivers Rhine, Meuse and Scheldt. He remarked that samples containing E. sanguinea nearly always contained L. conchilega and suggested a possible commensal relationship. He did not, however, find E. sanguinea inside tubes of Lanice. Clark (1960) recorded E. sanguinea (as Eulalia sanguinea) from Kames Bay among Laminaria holdfasts (about low water spring) and from 20m where a sandy-mud bottom was covered with a layer of Laminaria debris. Korringa (1951) placed E. sanguinea amongst the normal inhabitants of the shell of the oyster. Eagle (1975) recorded E. sanguinea (as Eulalia) from below 6m in Liverpool Bay and mentioned that E. sanguinea lived in empty Lanice tubes. Interestingly, Eagle found that Eumida was more abundant in samples

with less fines. Buhr (1979) also reported E. sanguinea (as E. punctifera) from Lanice tubes and although he did not specify empty or occupied tubes he did state that according to laboratory investigations (no details given), E. sanguinea nips bits off the tentacles and abdomen of Lanice. A.J.M. Walker (pers. comm., 1979), who worked with Eagle, also suggested this possibility. Buhr recorded a mean abundance of 33.5 individuals m^{-2} (range 5-425 m^{-2}) from a subtidal Lanice association.

Fauchald and Jumars (1979) postulated that all phyllodocids are hunting predators and scavengers, feeding on a variety of small invertebrates and carrion. It is clear from the distributions detailed above that Eumida inhabits structurally heterogeneous environments (Lanice tubes, Laminaria holdfasts and debris, oyster shells) and could be described as a cryptic (concealed in crevices, tubes, detritus) scavenger or carnivore. E. sanguinea was found in occupied Lanice tubes from Tentsmuir and observed to withdraw from the tentacles of Lanice when outside the tube (as opposed to H. lunulata which immediately re-entered the tube). This suggested to me that Eumida did not have an entirely easy relationship with Lanice and I conducted a simple experiment (described in section 5.3). The result of the experiment, although not replicated, indicated that Eumida may indeed have fed on Lanice but the construction of a tube offered some degree of protection.

Harmothoë lunulata

Harmothoë lunulata was present in less than half of the infaunal samples from Tentsmuir and never exceeded 5 individuals in any sample (Table 5-1). The relatively low abundance does not reveal much about the distribution but three of the four samples with four or more Harmothoë were collected in August 1978 and all were from algal-Lanice mounds or Lanice flats. No Harmothoë were collected from pools, drainage channels or megaripples. Harmothoë was associated with high Lanice abundance and high Lanice tube density (Table 5-2). This association is to be expected as Harmothoë was usually found in occupied Lanice tubes. The average density of H. lunulata at Tentsmuir was 28 individuals m^{-2}.

Wolff (1973) reported that in the deltas of the rivers Rhine, Meuse and Scheldt, H. lunulata was only found in the tubes of L. conchilega, often in considerable numbers. In the delta areas it was found from 5-32 m depth. Clark (1960) recorded H. lunulata as widespread on a wide variety of substrates in the sublittoral (1-168m) and intertidal on the Isle of Cumbrae. Hartmann-Schröder (1971) described H. lunulata as commensal with L. conchilega (and other polychaetes, enteropneusts, sipunculids and echinoderms) and very widespread from the intertidal to 990 m depth. Hartmann-Schröder (1971) considered H. lunulata to be a cryptic species, living in cracks and holes on hard ground and empty polychaete tubes. Buhr (1979) found Harmothoë spp. (H. lunulata and H. imbricata) in Lanice tubes with a combined abundance of 31.8 individuals m^{-2} (range 5-180 m^{-2}).

Polynoids are generally considered to be carnivores (see Fauchald and Jumars 1979 for review) and most of them are commensals. Davenport (1953) found a polynoid 'attractant' associated with the exterior of terebellid hosts and reported that populations of H. lunulata are strongly attracted to specific hosts (he did not test against Lanice). Fauchald and Jumars (1979) considered the curious combination of carnivores commensal with selective deposit-feeding hosts (such as Lanice) and suggested that the commensal need not necessarily feed on the host (which is strictly an ecto-parasitic relationship) but may feed on the food or pseudofaeces of the host. I suggest that they may also use the tube as a refugia and feed opportunistically on the wide variety of food available in the structurally heterogenous habitat around Lanice tubes.

Anaitides maculata

Anaitides maculata was present in 39% of the infaunal samples from Tentsmuir and only twice exceed five individuals in any sample (Table 5-1). This low abundance does not allow a clear evaluation of the distribution, but both high abundance samples were collected from algal-Lanice mounds. No A. maculata were collected from the drainage channel or megaripples and only one from the pool. Interestingly, only one A. maculata was collected in August 1978 (the period of greatest Eumida abundance). Anaitides was associated with high Lanice abundance and high Lanice tube abundance (Table 5-2). This association is to be expected as Anaitides was found in occupied and unoccupied Lanice tubes. The average density of A. maculata at Tentsmuir was 54 individuals m^{-2}.

Wolff (1973) considered A. maculata to be an inshore species found in poorly sorted and muddy sand (as opposed to A. groenlandica found offshore in cleaner sand). In his samples, A. maculata ranged from high in the intertidal to 48m. Clark and Milne (1955) reported A. maculata only below low water in muddy sand with maximum density at low water spring level, but Wolff (1973) attributed this truncated distribution to the nature of the substratum in Kames Bay (sand above L.W.S.T. and muddy sand below). Clark (1960) recorded A. maculata as common at L.W.S.T. on sandy beaches, but his records are primarily from Kames Bay and White Bay. Hartmann-Schröder (1971) reported A. maculata in a wide variety of substrata (amongst algae, in rock-pools, mussel- and oysterbanks, gravelly mud, sand, and muddy sand) from the intertidal to the sublittoral. Eagle (1975) found high abundances of A. maculata (his Phyllodoce mucosa, was later re-identified as A. maculata by A.J.M. Walker, A.J.M. Walker pers. comm.) associated with L. conchilega and E. sanguinea. Buhr (1979) was not certain of the distinction between A. maculata and A. mucosa but reported a combined abundance of 12.6 individuals m^{-2} (range 5-90 m^{-2}) in 39% of his samples.

A. maculata has been reported as a predator, particularly on other polychaetes (Evans 1971 as P. maculata, Hartmann-Schröder 1971) but Fauchald and Jumars (1979) supported the view that phyllodocids may also scavenge, eating carrion as well as live prey. A. maculata appears to inhabit structurally heterogenous substrata (i.e. avoids clean, well-sorted sand or mud preferring a mixture or a rough bottom) and could be described as a cryptic scavenger or carnivore (like E. sanguinea). A. maculata was found in occupied and unoccupied Lanice tubes which suggested

a parasitic or commensal relationship. The results of the feeding experiment (described in section 5.3) indicated that Anaitides can feed on Lanice although it is not clear what caused the death of Lanice in each case. A. maculata was not successful, however, in attacking any Lanice provided with building material. This seems to indicate that A. maculata is more of an opportunist than a direct predator on healthy Lanice.

5.2 Reproduction and recruitment

5.2.1 Larval development and settlement of Lanice conchilega.

The development and reproduction of Lanice conchilega was carefully investigated and described by Kessler (1973). She ably reviewed previous investigations and was the first investigator to trace the development from the fertilised egg through to the bottom-living juvenile. This work established a direct connection between the planktonic, tube-dwelling larvae commonly described as L. conchilega (Thorson 1946) and the benthic, tube-dwelling adult L. conchilega. The following details of the larval development and settlement were derived from her detailed description and personal observations.

Lanice conchilega is dioecious (the sexes are separate) and the sexually mature worms are easily distinguished. The males and females are mature from April to the end of June in Sylt (German Bight, Kessler 1973). The developing gametes are carried in the coelomic fluid. Male gametes are visible through the thin walls as a milky-white mass and the female gametes as red-brown globules. The ripe gametes are released directly in the water where fertilisation occurs. The fertilized egg develops into a free-living trochophore larva (a tiny animal with a conspicuous tuft of cilia at the top) and quickly metamorphoses into a worm-like aulophore larva (Figure 5-21a).

The aulophore larva is formed 6-10 days after fertilization. During metamorphosis the larva begins to build a simple tube of mucous and detritus, this develops into a characteristic, mucous tube when the metamorphosis is complete (Figure 5-21b). The tube is secreted by an exclusively larval structure, the dorsal gland, and is composed of sulphated mucopolysaccharides (Tiberi and Vovelle 1975). The tube is apparently built successively forwards as the larva develops and grows. This results in a tapering form, open at both ends, with oblique layers visible in the wall of the tube. The form is similar to the tube of Lagis koreni but is composed of mucopolysaccharides without detrital grains.

The aulophore moves constantly within its clear tube as it is carried by currents in the plankton. Lanice has a prolonged larval life, and this planktonic stage may last up to 2-3 months (Thorson 1946). The long planktonic life results in large-scale dispersal and aids in the spread of the offspring of a particular parent (siblings). Strathmann (1974) has suggested that this type of dispersal is advantageous when success in survival and reproduction varies independently from place to place.

During the period of planktonic life the rudimentary organs of the aulophore develop into gills, setae, setal hooks, mouth, lips and prostomial tentacles. When these organs are completed the larva will settle and begin a benthonic life, however, the exact timing and mechanism of this change is not known. At the time of settlement the extensile, prostomial tentacles are usually well-developed (Figure 5-21c) and capable of the same coordination as in the adult.

After settlement the worms, here considered juveniles, burrow into the sediment in exactly the same manner as adult worms removed from their tubes. The larval tube (or in the case of adults a loose, mucous tube produced by rolling from side to side) serves as a surface for exerting hydrostatic pressure through peristaltic waves of the body (König 1948, Seilacher 1951, pers. obs. 1977). The propulsive force of the hydrostatic waves are directed vertically downward into the sediment and the prostomial tentacles help push and mould the sediment particles into a mucous-lined tube. The initial tube is a u-shape as the young worm burrows for 1-3 cm and turns back up to the surface. The tube is then extended above the substratum and decorated with a tiny fringe like the adult tubes.

Juvenile L. conchilega were observed in a ridged photography tray after collection with a plankton net in May 1980. Well-developed autophores in their clear larval tubes were placed in the tray which was covered with gauze and left on a sea-table for 48 hours. A suspension was prepared of filtered seawater and sediment which settled out of the continuously flowing seawater system of the Gatty Marine Laboratory. The seawater system has an intake on an exposed beach (East Sands, St. Andrews) which received a periodic influx of suspended sediment from a small stream and harbour (Kinnessburn, St. Andrews Harbour). Organic-mineral aggregates and very fine sand settled out of the seawater and provided material for tube-building and deposit-feeding.

After 48 hours most of the larvae had settled and built tubes of mucous and detritus. The tray was rinsed with clean seawater and photographed before it was re-filled with a seawater-sediment suspension (Figure 5-22a). The tray was left to settle for 12 hours and photographed at 2 hour intervals until deposit-feeding activity appeared to cease (36 hours). The tray was not an ideal culture dish as the sediment settled unevenly and the worms were not able to build natural, vertical tubes. The results, however, provided a rough estimate of the feeding radius in juvenile L. conchilega.

The worms began gathering sediment within 1 hour of the addition of new sediment (they had been feeding before the tray was rinsed) and by 12 hours, distinct patches of unevenly cleared sediment appeared. The clearing efforts were marked by ring-shaped clusters of faecal material at the ends of detritus tubes (Figure 5-22b). As the faeces built up and the sediment was cleared from a wider area, the centre of the doughnut-shaped ring was filled with faeces and surrounded by a cleared ring up to 1 cm across (Figure 5-23a, 18 hours). Many worms built branched tubes and switched their deposit-feeding activity from end to end as adjacent cleared areas began to intersect (compare cleared areas around single tubes in Figure 5-23a with the same areas in Figure 5-23b); in all cases both areas have increased).

It is not known what proportion of the sediment was actually ingested and what proportion was merely sorted for particular particles. The worms clearly sorted some sediment to provide building materials for vertical tubes (Figure 5-24a). These vertical tubes began to appear after the

sediment supply decreased (because of limited tentacle range) and although some worms responded to the decrease by extending the horizontal tubes (Figure 5-23b, fr), most of the worms had begun to construct vertical tubes of the largest grains available (0.125 mm) after 24 hours.

The settlement behaviour of the young L. conchilega may be influenced by the presence of the adult tube, either hydrodynamically through entrainment in local areas of disturbed flow or chemically through some attractant in the tube or secreted by the adult worm. Neither of these possibilities have been investigated specifically, but observations on the flow disturbance of single and paired tubes in unidirectional flow are discussed in Chapter 6. The settling worms apparently find the adult tubes attractive substrata, small tubes were commonly found clustered around larger, older tubes (Figure 5-24b, see also washed core and detail in Figs. 4-10, 4-11).

There was no evidence that the adult's deposit-feeding activity prevented the young worms from successfully settling within the radius of their tentacles. Dr. Ziegelmeier (pers. comm., 1978) suggested that the size of the bottom-stage larva (the fully-developed aulophore tube measures 1.6 mm long and 0.15 mm in diameter) prevents the adult from ingesting the young worms. Gut dissection of mature adult L. conchilega from Tentsmuir Beach revealed no particles larger than 0.5 mm (mean grain size 2.4 phi, appeared to have reflected mean grain size in surface sediments, 2.24-2.36 phi but the sample was very small n=5). The successful recruitment of large numbers of young worms into an established population of older worms (also reported by Buhr and Winter 1977, Buhr 1979) may have been responsible for the continuity of the patches observed at Tentsmuir

(>15 years) and the subtidal population in the Weser estuary (13 years, Buhr and Winter 1977).

As the young worms grew they left their initial narrow, u-tubes and constructed larger tubes. This process of renewing the tube as growth occurs apparently continues throughout the life of the worm (Ziegelmeier 1952, Schäfer 1972). It is possible that at this stage some spacing may occur from the initial cluster about the adult. Adult tubes of single size class and size class mixtures (excluding the smallest, initial tubes) were only rarely observed to be in contact along their length. Tube tops were observed to be spread relatively evenly at densities above 2000 m^{-2} (Figure 5-25) but this apparent regular distribution may be a random filling of the available space with cylinders that cannot overlap (see Simberloff 1979).

L. conchilega reproduces over a long period (larvae in observed plankton from April-October, Wolff 1973) by releasing large numbers of planktonic larvae (up to 2.8 larvae in water under 1 m^2 surface area, Elbe estuary, Kühl 1972), which will settle on a variety of substrata but apparently prefer aggregating near established adults.

5.2.2 Larval development and settlement of other species

Polychaetes

Eumida sanguinea, Anaitides maculata and Scoloplos armiger all spawn eggs in jelly-like cocoons (Wolff 1973). These cocoons are a conspicuous feature on the sediment surface from mid-February to June at Tentsmuir Beach. Although the primary function of the cocoon-forming habit in S. armiger is considered to be prevention of the wide dispersal of larvae, the eggs of E. sanguinea and A. maculata hatch into planktonic trochophores (Chapman 1965, Gibbs 1968). The free-living trochophores, positively phototactic in A. maculata (move toward light, Chapman 1965), should permit wide dispersal and remove any advantage in localised egg-masses. It is not clear what advantage the egg-masses provide, they may simply provide a suitable environment for the developing eggs, however, it cannot be discounted that the planktonic stage is restricted in favourable conditions. The egg masses were commonly found attached by stalks to Lanice tubes, but the presence of aggregated populations of adults and newly-settled juveniles amongst the tubes may be a result of a more complex dispersal and settling behaviour.

No details are available on the reproduction of Harmothoë lunulata, but the embryos of H. imbricata are protected during their early development (unfertilised egg - trochophore) as a mass under the scales of the female parent and releases planktonic larvae into the water (Daly 1972). If this method of brood protection is common to all Harmothoë spp., then H. lunulata would seem to have a life-history similar in some

respects to both E. sanguinea and A. maculata.

The breeding behaviour of Nephtys cirrosa and Ophelia limacina are not known, but they have been assumed to have planktonic larvae without brooding (Wolff 1973). The development and settlement of O. bicornis was described in detail by Wilson (1948 a, b) and the nectochaetae and bottom stage larvae of H. hombergi have been described by Rasmussen (1973). O. bicornis showed strong substratum specificity in experiments conducted by Wilson (1955) who concluded that the most important factor in inducing settlement was the presence of living microorganisms on the surface of the sand grains. Wolff (1973) emphasised the substratum specificity of Nephtys spp. based on ecological distributions and it may be surmised that Nephtys can also choose attractive sediments during settlement.

Although the evidence is limited, the dispersal and settlement of the common polychaetes at Tentsmuir may be divided into those with apparent Lanice associative settlement (sensu Crisp 1979: settlement in response to another species): H. lunulata, A. maculata, E. sanguinea; and those with apparent substratum associative settlement (settlement in response to microorganisms on the substratum): N. cirrosa, O. limacina.

Bivalves

No information is available on the substratum selectivity of Tellina tenuis. T. tenuis has been observed to spawn between June and September in Firemore Bay (Trevallion 1971) and both over-dispersed (spaced, Holme 1950) and under-dispersed (aggregated, Stephen 1930) populations have been reported. Reproduction in T. tenuis has been seen to be limited by

cropping of siphons by plaice (Pleuronectes platessa, Trevallion et al. 1970) and appeared to result in failure of recruitment (McIntyre 1970). Trevallion (1971) extended this discussion and concluded that when food is limiting, siphon predation causes a greater drop in 'condition' than can be due to a loss of siphon tissue alone, and that condition and recruitment are probably connected with changes in other organisms in the environment.

It is clear when examining detailed evidence from long-term population studies, such as the T. tenuis study in Loch Ewe, that simple explanations of settlement, growth and mortality are not sufficient to account for variations in abundance of local populations. This is abundantly clear when examining variations in abundance and distribution of components of a community such as the one studied at Tentsmuir Beach. Any conclusions from this study must be very tentative and should be followed by intensive studies of individual species.

5.2.3 Transplant experiment

In order to examine the influence of the presence of Lanice conchilega on the settlement of all infaunal species, a simple transplantation was performed in April 1979. A large area of Lanice tubes was dug with a garden fork and the intact tubes sieved with a 2 mm sieve. The tubes were examined in the lab and short (2-3 cm) sections prepared containing intact L. conchilega. This was done by gently pulling off 2 cm sections of tube until the worm was isolated in a small section. These tube sections were

examined carefully and any polychaetes other than L. conchilega were removed. Large numbers of E. sanguinea, A. maculata and H. lunulata were observed in this way and provided material for the experiment described in section 5.3.

The site selected for transplantation was north of the transect (see Figure 2-4 for location) in an area of small ripples and very low Lanice density. The site had been an algal-Lanice mound in April 1978 but the tubes and algae were removed by storms in the winter of 1978-79. Thus, the site was in an area with suitable conditions for Lanice but at the time of the transplant had few Lanice present. Two samples of 4 can-cores each were removed from sites directly adjacent to the transplant site to record the pre-existing fauna (LTC1, LTC2).

2000 sections of Lanice tube were prepared and placed in the transplant plot at a density of 0.5 sections cm^{-2}. This was done with the aid of wire mesh grid, 40 cm x 100 cm, with 1 cm mesh. The grid was placed on the sediment surface parallel to the crests of ebb current ripples (presumed to be perpendicular to the dominant flow direction). Tube sections were placed in alternate 1 cm^{-2} areas of the grid and were lightly pushed into the sediment. Trials with glass rods and tubes (Ziegelmeier 1969) failed on the beach in packed sand. The grid was left staked in place for 24 hours. At this time the worms had established new tubes and the grid was removed. A control plot was also staked with a grid and the surface was disturbed in alternate 1 cm^{-2} areas, but no tubes were placed in the control area. It was felt at the outset of the experiment that placing unoccupied tubes or artificial tubes was not feasible due to the high rate of sediment movement (pins 30 cm long were placed along the

transect in 1977 and none were recovered 1 month later).

The transplant plot developed into a small algal-Lanice mound, whereas the control plot remained as a small ripple field. Other small algal-Lanice mounds were observed 2-5 m from the transplant plot. In October 1979 four can-cores were removed from the transplant plot and four can-cores were removed from the control plot (LTT1, LTC3, respectively). The infaunal species were recorded from all samples and the incidence of Lanice tubes with attached juvenile tubes was recorded from samples LTT1 and LTC3.

The samples collected before the transplant (April 1979) contained a typical infauna from a small ripple field with the exception of unusually high numbers of Mytilus edulis spat (Table 5-4). When the spat are excluded the total abundances (LTC1: 68, LTC2: 64, both in 0.08 m^2) were lower than total abundances recorded from small ripple fields in March 1979) (5f: 126, 6f: 91, both in 0.08 m^2, Figure 5-12). The numbers of species (including M. edulis) were comparable to species numbers in small ripple samples (LTC1: 6, LTC2: 7; 5f: 8, 6f: 7, Table 5-4 and Figure 5-4).

The control sample taken six months after the transplant (LTC3, October 1979) showed an increase in abundance and no change in the number of species, although different species were present (Table 5-4). There was some recruitment of Lanice as 12 juvenile tubes were recorded attached to unoccupied adult tubes and 7 out of the 9 L. conchilega were 1979 settlement (Table 5-5). No recruitment of E. sanguinea, A. maculata, or H. lunulata was recorded although the former two species were recorded as

adults in one of the March 1979 samples. Recruitment of S. armiger was observed as one juvenile was recorded but no other species were recorded as 1979 settlement. No small ripple fields were sampled in October 1978, but the total abundance of the control sample after the transplant was lower than the pool sample in October 1978 (see Figures 5-10 and sample 3p in Appendix Table I).

The sample taken from the transplant plot (LTT1) six months after the transplant (October 1979) showed an increase in abundance and number of species over both of the March 1979 samples and the control plot sample (Table 5-4). There was an overall decrease in Lanice density from the transplant density (5000 m^{-2} in transplant, 962.5 m^{-2} in October) but considerable recruitment of young L. conchilega. This is an indication that a large proportion of the transplants may not have survived the initial placement and less than 7% survived until October (25 of the 77 worms were adults = 312.5 m^{-2} = 6.25% of 5000 m^{-2}). The recruitment is seen in Table 5-5 where 52 of the 77 worms (68%) were 1979 settlement and 26 juvenile tubes were recorded attached to 17 adult tubes. Recruitment was also observed in E. sanguinea, A. maculata and S. armiger populations where all the individuals recorded were 1979 settlement. The abundance of T. tenuis was much lower than any of the control samples and no recruitment was observed in this population or the N. cirrosa and O. limacina populations. The reason for the decrease in T. tenuis is not known as both plots were disturbed, but T. tenuis is capable of dispersion after settlement so the increased disturbance from the introduced L. conchilega may have had an influence. A negative association between Lanice and Tellina was not observed in the transect samples.

Juvenile M. edulis, C. crangon and A. rubens were also observed in the transplant plot sample. All of these species are only temporary residents but it is interesting to note their presence in the transplant plot and their absence in the control plot.

The total abundance (without M. edulis) of the transplant plot sample (141, Table 5-5) was lower than the total abundance of islet or Lanice flat samples in October 1978 (175-354 in 0.08 m^{-2}; Figure 5-10). This was primarily because of low L. conchilega abundance in the transplant plot. The number of species (with M. edulis) was, however, higher than in any sample in October 1978 (range 3-5 species, Figure 5-4).

The transplant experiment was not conducted with sufficient controls to determine which of many factors may have been responsible for increased recruitment in the plot occupied by introduced L. conchilega. It was demonstrated, however, that the transplantation procedure was successful in replicating an algal-Lanice mound and inducing increased settlement of L. conchilega and associated species. I would suggest transplantations of tube-building polychaetes are a viable field experimentation technique, providing that sufficient numbers of healthy worms are available for replication. I would further suggest that the sediment in similar plots could be entirely replaced with dried, seawater soaked sediment and seeded with adults in tubes as a further control. These experiments should be conducted in parallel with laboratory investigations of settlement behaviour and substratum selectivity in each species of interest.

5.2.4 Larval settlement dynamics

Aggregated settlement, gregarious settlement (in response to adults or juveniles of the same species) and habitat selection are widespread phenomena in marine invertebrate species (for reviews see Thorson 1946, 1966; Gray 1974; Scheltema 1974; Crisp 1979). Crisp (1979) has argued that larval dispersal and subsequent re-aggregation requires substantial energy for reproduction and must therefore provide an advantage. He suggested that high genetic variability and choice of settlement site enable species to fill a wide range of niches and for some species larval transport allows risk in colonising unstable habitats. Larvae may actively choose their settlement sites (see Meadows and Campbell 1972 for reviews) or may be passively deposited (or aggregated) by hydrodynamic forces; in many cases a combination may occur (Hannan 1981).

In addition to primary settlement some newly settled larvae are able to survive disturbance or actively leave a settlement site and settle on a second site. Young post-larval bivalve molluscs have been shown to enter a second pelagic phase (Baggerman 1953, Bayne 1964) and this secondary redistribution is aided by secretion of byssus threads which increase form drag and promote transport in tidal currents (Titman and Davies 1976, Frenkiel and Mouëza 1979).

The details of active habitat selection and/or hydrodynamic deposition have not been investigated in the present study. It is, however, worth considering possible mechanisms and advantages of the aggregated settlement observed for Lanice. Eckman (1979) postulated the influence of flow around

needles (1 mm in diameter, simulating worm tubes) on the distribution of infaunal species. He found that a tanaid and a polychaete were aggregated around the needles and suggested that regions of low flow velocity around the needles may have created small-scale environmental heterogeneity which affected the species dispersion.

Fager (1964) attributed the concentrations he found of Owenia fusiformis (tube-building polychaete) to the effects of rip-currents on settling larvae. Other tube-building polychaetes which form an aggregated mass but cement adjacent tubes together (Sabellaria alveolata), have a gregarious behaviour in settling: they are influenced by the cement secreted by new metamorphosed or adult worms (Wilson 1968). S. alveolata, however, also responds to hydrodynamic factors: the initial stimulus for larval settlement was demonstrated by Wilson (1968) to be vigorously moving water carrying sand in suspension. Tyler and Banner (1977) suggested that the distribution of echinoderm larvae in Oxwich Bay could be explained by passive deposition from tidal currents. Hannan (1981) considered this possibility as an explanation for higher densities of larvae in suspended jars than in adjacent substrata and suggested that a combination of active selection and passive deposition may have produced her results.

The observed settlement patterns of L. conchilega (juveniles clumped around adults) may be in part due to hydrodynamic aggregation in the vicinity of the tubes and in part due to active selection of the adult tubes or tubes of previously settled juveniles. Young post-larval Mytilus edulis (spat) were also found settled in clumps on the tubes and have been well-documented as utilising a mechanism of secondary redistribution through byssal drift (Bayne 1964, Titman and Davies 1976). The larvae of

Lanice are capable of considerable movement, postponement of settlement and have well-developed sensory appendages (Kessler 1973), but they are easily transported by tidal currents in their large transparent tube. This tube may act as a low density sediment particle and be passively deposited but larva presumably still have to respond to a stimulus to burrow or not to burrow.

Unlike Sabellaria alveolata which remains close to its settlement site, L. conchilega appeared to space out after the initial aggregation. The advantage of spacing out can be seen clearly in Figure 5-24b where young, settled worms have cleared areas up to 1 cm in diameter and switched between potential areas in deposit-feeding. Overlap of deposit-feeding areas would not be desirable, but hydrodynamic investigation has shown that there may be an optimal spacing for suspension-feeding (Chapter 6). Small-scale spacing out associated with gregarious settlement has been described from purely suspension-feeding polychaetes (Spirorbis borealis, Knight-Jones 1951; Wisely 1960; Harvey et al. 1976).

Buss (1979) has suggested that habitat selection may evolve when the location of a spatial refuge can be sensed by the recruiting larvae. The behaviour of E. sanguinea, A. maculata and H. lunulata as cryptic species and opportunistic carnivores suggests that they are more likely to respond as larvae to a spatial refuge than to specific cues released by L. conchilega, but their settlement behaviour is not known.

5.3 Predation

Several important, preliminary observations were made on the effects of predation on the infaunal community at Tentsmuir Beach. These observations will be discussed in the context of more detailed studies conducted in similar environments. Important reviews include the recent volume devoted to feeding and survival of estuarine organisms (Jones and Wolff 1981) which mainly considered bird predation, the review by Arntz (1980) on predation by demersal fish, and the review by Bonner (1972) on the European grey seal and common seal. Literature on predation by invertebrates is more complex and scattered but Dayton and Oliver (1980) provided an excellent critique and review of predator exclusion experiments, Hughes (1980) reviewed a wide range of effects of predation on community structure and predation strategies and Fauchald and Jumars (1979) reviewed feeding in polychaetes.

Investigations into the establishment and maintenance of dense infaunal assemblages (such as the dense Lanice association described above) have identified predation and disturbance as important factors (Woodin 1978, Peterson 1979, Virnstein 1979). The effects of predation and biological or physical disturbance on the structure of marine benthic communities have largely been surmised from exclusion of predators by caging portions of the bottom or removal of predators from a large area. These manupulative experiments have had equivocal results in soft-bottom environments and the widespread application of the hypotheses and paradigms derived from these studies is not advised. Dayton and Oliver (1980) have urged the proper use of experimentation to falsify rather than verify

hypotheses, I must concur with this argument and add that careful observations and surveys are important prerequisites to manipulation of any unknown habitats.

It is not intended here to give an exhaustive discussion of the many hypotheses of the factors influencing soft-bottom benthic community structure (Dayton and Oliver 1980 and Gray 1981 provided excellent reviews), but rather to comment on observations of the Lanice conchilega association which appear to contradict some of the assumptions and support others and to suggest possible directions for further investigations. The data presented in this chapter are valuable as background to an important type of infaunal community which until recently has received little attention.

5.3.1 Invertebrate predation

The primary epifaunal invertebrate predators on infauna in many intertidal sand and mud habitats have been reported to be crabs (Woodin 1978, Reise 1978, Virnstein 1977, 1979, Holland et al. 1980). Many attempts have been made to investigate the effects of predation by epifaunal animals on infaunal community structure through the use of predator exclusion cages (see Dayton and Oliver 1980 for review). The cages have serious artifacts because of the importance of hydrodynamic equilibrium in all depositional environments (Virnstein 1978). It is impossible at present to determine whether the results from these caging experiments are from the exclusion of predators or from a multitude of

changes in the substratum caused by interference in the natural flow conditions. Cages proved particularly inappropriate at Tentsmuir where the strong currents and large amounts of detrital macroalgae quickly removed artificial structures. No attempt was made to exclude epifaunal predators for these reasons but Reise (1978) in a well-balanced field and lab study of interidal habitats in the Wadden Sea concluded that the main vagile invertebrate predators were Carcinus maenas and Crangon crangon. The fauna represented in his study was very similar to that present at Tentsmuir and although he did not study any habitats with strong currents it seems likely that Carcinus and Crangon were also important predators at Tentsmuir.

Another important effect of invertebrate predation may be the exclusion of settling larvae through ingestion by deposit-feeding or suspension-feeding adults. Woodin (1976) presented the hypothesis that dense infaunal assemblages are maintained through interactions among established infaunal adults and settling larvae. Field and laboratory experiments have demonstrated that dense assemblages of deposit-feeders may restrict settlement and survival of suspension-feeders through reworking of surface sediment causing clogging of suspension-feeding mechanisms and smothering of settling larvae (Rhoads and Young 1970, 1971). Woodin (1976) predicted that dense assemblages of tube-building species should exclude all settling species (including their own) apart from small epifaunal bivalves that brood their young. She suggested that this would occur through restriction of infaunal space and ingestion and/or continual disturbance of larvae through defecation and feeding activities. No field studies have supported this hypothesis but Wilson (1980) reported from lab experiments that the survivor-ship of the larvae of Nereis vexillosa was significantly lowered by the feeding activities of Eupolymnia

heterobranchia (terebellid polychaete). He suggested that E. heterobranchia ingested the larvae of N. vexillosa. Although it is possible that Lanice may also ingest larvae of polychaetes it is clear from the field results discussed in Section 5.2 that Lanice does not exclude either its own settling larvae or the larvae of E. sanguinea, H. lunulata or A. maculata. There was no evidence that Lanice ingested or excluded any larvae but detailed experiments were not performed.

The suggestion of Buhr (1979) and Walker (pers. comm.) that E. sanguinea and A. maculata may feed on Lanice tentacles while sharing the tube was investigated in a simple lab experiment. The details of the experiment and the results are presented in Table 5-7. Unfortunately sufficient numbers for replicates of E. sanguinea trials were not available but it is clear from the results that the presence of a tube is an important factor in the protection of Lanice from infaunal predators. The exact cause of death in each trial is not known, but these results support the suggestion that A. maculata and E. sanguinea can feed on Lanice. It is possible, however, that they would not feed on Lanice in normal field circumstances as the Lanice provided with tube material did not appear damaged in any way despite being confined with a carnivorous polychaete for 65 days.

These results are a further indication that the provision of a spatial refuge (tube in this case) is an important factor for the survival of Lanice. The importance of spatial refugia has been emphasized by Brenchley (1976), Woodin (1978), Virnstein (1979) and Wilson (1979), in each of these studies tube-building polychaetes in sandy habitats have escaped predation or disturbance by retraction into the tubes or simply through the

structural effects of the tubes themselves.

5.3.2 Fish predation

No attempt to investigate fish densities or predation at Tentsmuir Beach was made in this study, but large numbers of 0-group (1st year) plaice were observed in the pools during June, July, August and September. Casual investigation of stomach contents of plaice indicated that Lanice and Tellina were major prey species and this necessitates some discussion. The feeding and migration of plaice in European waters have received considerable attention in recent years because of their commercial importance (Edwards and Steele 1968, Lande 1973, Thijssen et al. 1974, Kuipers 1977, Wolff et al. 1981). Flatfish nursery grounds are located in sandy bays and estuaries and the impact of the fish on the macrobenthos of these areas has also received a lot of attention (McIntyre and Eleftheriou 1968, Trevallion et al. 1970, Beukema 1974, 1976, Arntz 1980).

St. Andrews Bay is an important flatfish nursery ground (McIntosh and Masterman 1897, Harden Jones 1968). Adult plaice (Pleuronectes platessa) spawn in relatively discrete groups, one such group is located off the East coast of Scotland and a major spawning area is the Firth of Forth (including St. Andrews Bay). After metamorphosis (movement of the left eye) to the bottom-living 'flatfish' stage, the young plaice actively migrate into shallow water. Scottish plaice spawn from November to May, with a peak from February to March and the bottom-living stage is reached by about 45 days after hatching (Harden Jones 1968). These young fish are

restricted to very shallow water (<7 m depth) but older plaice migrate onto tidal flats during high tide (Wolff et al. 1981). The young plaice stay in shallow water for about six months before migrating to deeper water (>10 m depth; McIntosh and Masterman 1897). Immediately after settling on the bottom in Loch Ewe the young fish fed mainly on Tellina siphons and polychaete tentacles but within weeks they were taking whole polychaetes, amphipods and crustaceans (Edwards and Steele 1968).

Plaice migrate with the tide; at low tide they are found concentrated at low water mark (Gibson 1973); subtidal gullies (Kuipers 1977); and tidal channels (Wolff et al. 1981). At high tide they move rapidly upshore both at night and during the day, although most authors reported that feeding activity is very low in the dark as plaice are mainly visual feeders (Gibson 1973, Thijssen 1974, Arntz 1980). Feeding activity was also reported as minimal during low tide which was attributed to the low densities of prey species subtidally (Kuipers 1977). There does not appear to be any intrinsic reason for low feeding activity at low water, because Kuipers (1977) observed plaice to feed on the flats at water depths of 50 cm or more. He also concluded that the richness of the Waddensea tidal flats prevented a negative correlation between density and growth unlike the situation on British coasts (Edwards and Steele 1968). Plaice in British waters may need to feed during all states of the tide, whenever prey is available.

Plaice are opportunistic in prey selection, they appear to feed heavily on the most abundant prey item available (Lande 1973, Thijssen et al. 1974). In many cases this constitutes cropping of siphons of bivalves and tentacles of polychaetes, but cropping is most common in 0-group plaice

(Trevallion et al. 1970). Larger plaice are capable of capturing prey below the surface, and can extract whole Lanice from their tubes (Eagle 1975). They do this by biting off the tube top, placing their mouth over the open end and powerfully sucking out the contents (see Risk and Craig 1977). Tube tops and whole worms have been found in plaice stomachs from St. Andrews Bay (Krakonis pers. comm).

The most important effect of plaice on the Lanice community may have been the maintenance of cleared areas. This is purely speculative as no experimental evidence is available, but the opportunistic feeding habits and low water concentration of plaice may have combined to produce intense burrowing or feeding activity in the areas sparsely populated by Lanice. Plaice normally burrow in sand with a thin layer of sediment covering them (Wheeler 1980). This activity would not be possible in dense tube areas and the young plaice may have concentrated in the areas with few tubes. As settlement of Lanice progressed, the burrowing and feeding activity of the juvenile plaice may have prevented successful settlement of Lanice in these areas and contributed to the development of the pools. There is a possibility of a feedback mechanism as the tube areas increased in density and algal cover forcing the growing plaice into the clear areas and thus maintaining a sharp boundary, but this hypothesis needs very careful field experimentation. The pools were generally not as deep as Kuiper's (1977) observation of a minimum feeding depth of 50 cm, but this observation was made in the rich tidal flats of the Waddensee.

To investigate this proposed mechanism I would suggest a combination of field manipulation experiments and laboratory observations of plaice behaviour rather than the use of cages to retain or exclude plaice from selected areas. A survey of plaice and tube density could be conducted during slack tides, both high and low water in selected areas. The survey should begin before May to include the rapid increase in density of juveniles that occurs in the summer. Intensive sampling in replicate plots with high tube density and low tube density and mounds and depressions would permit manipulation experiments. Two forms of manipulation could be performed with appropriate controls in each area. Excavation of depressions and removal of all tubes should simulate the predicted optimum conditions for plaice. Disturbance of plots (excavation, seiving and replacement of sediment) followed by transplantation of tubes should simulate colonization of disturbed areas by settlement.

Plaice could be sampled with push nets (during low spring tides in the pools, during low neap tides in shallow water, and high tides by diving) and retained for examination of gut contents. Tubes could be sampled with small ($< 0.01\ m^2$) replicate cores and examined for damage and occupancy. On the basis of the hypothesis described above, I would predict less successful recruitment of tubes and increased plaice density in depressions and the reverse in mounds.

5.3.3 Bird predation

The location of the dense Lanice community was often apparent before the surface was exposed at low water because of the high densities of birds feeding in shallow water. The dense aggregations of Lanice tubes and the abundant fauna present in the study area appeared to influence the selection of feeding sites by waders, gulls, terns and eider ducks all of which were usually more abundant on the study area than on adjacent areas of the beach. Many waders use visual cues in the search for prey (Dare and Mercer 1973, Pienkowski 1981) and shorebirds are generally opportunistic predators feeding on the most abundant prey available (Goss-Custard 1977a, 1977b; Schneider 1978). Eider ducks migrate in flocks to feed on mussel beds at low water (Pounder 1971, Milne 1974) and gulls will attend these flocks to rob prey (Prys-Jones 1973).

Counts of birds feeding within the limits of the study area (ca. 15,000 m^2) were made upon arrival at the beach (usually about 1 hour before low water) and occasionally after flood. Additional, informal, observations were made on feeding behaviour and densities of feeding marks and droppings. Despite the lack of continuous detailed monitoring a seasonal pattern of predation in one species was discerned.

Eider ducks (Somateria mollissima) were observed feeding on the study area from March until late May. Eiders were observed in and around the Abertay sands and Tentsmuir Beach throughout the rest of the year but did not appear to be feeding on the study site. Groups of 10-50 eiders would congregate about 2 hours before low tide in the tidal channel and feed in

the shallow water as the tide receded. Individual birds fed at intervals such that some birds were feeding throughout the low tide period. If the eiders were not disturbed they continued to feed for approximately four hours or until the tide was well above neap low water. It is not known if the eiders returned to feed on evening low tides but a tidal feeding rhythm has been observed in other areas with a high tide range (Milne 1974) while in areas with a small tidal range, feeding is confined to early morning and late evening (Pethon 1967, Dunthorn 1971). Pounder (1971) studied the movements of wintering eiders in the Tay estuary (including Tentsmuir) and concluded that the daily movement of the flocks should be governed by the location of mussel beds and the depth of the water covering them. It seems reasonable to assume that the small flock of eiders that fed on the study area did return on evening tides and that the feeding activity was confined to four periods, approximately 2 hours either side of each low tide.

The feeding activity of the eider ducks consisted of excavating a crater in the submerged sand with their feet, up-ending and rooting about in the sand and tubes with their bill and apparently swallowing the prey underwater. Player (1971) observed similar feeding activity on mud substrata at Seafield, Firth of Forth. Dunthorn (1971) observed eiders feeding intensively on mussels growing on suspended ropes and reported that the ducks swallowed the mussels (up to 60 mm long) underwater. The activity at Tentsmuir produced circular depressions in the sand up to 0.5 m in diameter (mean 0.24, n=27) and 15 cm deep. Once the surface of the study area was exposed, the flock moved into the tidal channel and ceased feeding, on no occasion were ducks observed feeding on the exposed surface.

In March 1979 either browsing traces were counted on 6 transects to the north of and parallel to the established transect (see Appendix Figure I for location). Each count was made on an area 1 m wide and 30 m long (total area censused: 180 m^2). The mean abundance of traces per transect was 3.83 (range 2-6) which gives a mean density of 0.13 m^{-2}. The total number of holes over the whole study area on this occasion was 127, these were found in an area of 2700 m^2 which represents a much lower density (0.047 m^{-2}). The transects covered an area with a particularly high density of Lanice tubes, whereas the total count covered a variety of tube densities. Thus, the eiders may have concentrated their feeding activity in the vicinity of Lanice tubes but a more detailed analysis would be necessary to establish a clear association.

The 127 holes were produced by 24 eiders feeding for 107 minutes. To accomplish this each eider would have had to produce one hole roughly every 20 minutes. If this is taken as an average rate and 0.25 m as the average hole diameter then a flock of 25 eiders would produce 300 holes covering an area of 58.8 m^2 in a 4 hour feeding period. This represents 2.29% of the observed feeding area, and although nothing is known about the persistence of this aggregated feeding activity this figure can be taken as a rough estimate of disturbance per tidal cycle.

Two samples were collected in March 1979 to assess the effect of eider browsing activity on infaunal species density. One sample (EBT1) was collected from the centre of an eider browsing trace and the other sample (EBT2) was collected 0.5 m from the centre of the same trace. The trace measured 0.43 cm in diameter and was disturbed to a depth of 5 cm. Two

species (Mytilus edulis, Carcinus maenas) which were abundant outside the trace were dramatically reduced or absent inside the trace (Table 5-6). Both of these species were present as juveniles on the tube tops and are not strictly speaking infaunal species. It is not known whether they were displaced or ingested during the feeding activity but both species are reported as important prey species of eider ducks (Pethon 1967, Dunthorn 1971, Pounder 1971, Milne and Campbell 1973).

The eiders apparently adopt the excavating feeding method at Tentsmuir to dislodge epifaunal organisms and uncover infaunal organisms. Eiders are well-known as specialist feeders on mussels and will adopt very circumscribed behaviour when mussel beds are readily available (Pounder 1971, Milne 1974). The increase in number of eiders in Scotland has been associated with the presence of mussel beds (Baxter and Rintoul 1953, Tavener 1963) and Milne (1969) considered the food supply to be the ultimate factor in population control. Thus, although it is likely that the eiders ingested other bivalves (T. tenuis, D. vittatus, C. gallina and C. edule were all reduced in the trace) and polychaetes (O. limacina is notable for its absence in the trace) I would suggest that the primary prey was the mussel spat and perhaps secondarily young C. maenas. L. conchilega and the associated polychaetes (E. sanguinea, H. lunulata, A. maculata) were not likely to be directly affected by eider browsing as they could all escape quickly down the long tubes, but the disturbed substratum and tubes could have been a strong attraction to waders and gulls after emergence. It is interesting to note that in the undisturbed sample (EBT2) 3 A. maculata, 1 O. limacina, and 1 H. lunulata were found in Lanice tubes whereas none were found in tubes in the disturbed sample (EBT2). Eider browsing activity clearly could affect the community

structure through disturbance and selective predation but the data presented here are not sufficient to draw detailed conclusions. The interaction between high density tube building polychaetes and large disruptive predators merits further investigation.

Five species of waders were observed feeding on the study site (oyster catcher, Haematopus ostralegus; dunlin, Calidris alpina; curlew, Numenius arquata; bar-tailed godwit, Limosa lapponica and grey plover, Plurialis squatarola), undoubtedly other species escaped notice. Of these species, oyster catchers were the most commonly sighted. Three of the species mentioned above are of particular interest as they were reported by Goss-Custard et al. (1977a) as selectively preying on Lanice. In a series of detailed experiments and observations in the Wash (in an area very similar to Tentsmuir Beach) Goss-Custard and his co-workers established that curlews, bar-tailed godwits and grey plovers fed extensively on dense Lanice beds when the beds were exposed (Goss-Custard et al. 1977a). These same birds reduced Lanice density outside exclosures (Goss-Custard 1977a) and declined in condition in winter, in part because of reduced availability of Lanice (Goss-Custard et al. 1977b).

Bird feeding activity was observed to occur during low tides at night in January 1979. Birds were not identified but fresh droppings, noise and abundant dead bivalves indicated wader and gull activity. Dugan (1981) discussed nocturnal feeding in shorebirds and advanced the tentative conclusion that for some species (grey plover) the major part of the energy requirements are met at night rather than during the day and that this, in part, was because of increased activity of prey species at night. Caution must therefore be exercised in any conclusions regarding bird predation

based on daytime observations.

Waders, gulls and terns all appeared to feed intensively on the study area, particularly following disturbance of the surface by storms, eider browsing or my own collection activity. Common terns (Sterna hirundo) and little terns (Sterna albifrons) were observed feeding on sand eels (Ammodytes tobianus) in the megaripple field in July 1978. Between 10 and 15 terns fed intensively for 30 minutes after the flooding tide had covered the study area (1 1/2 hours after low water). In April 1978 and subsequently low tides, waders (oyster catchers) were observed feeding on the dense population of Spisula solida in the megaripple field. Spisula, Ensis siliqua and Donax vittatus were all susceptible to heavy bird predation on low tides because of their curious habit of rising out of the substratum as the tide turned (see Figure 3-12a). It is not known what caused this apparently suicidal behaviour at Tentsmuir, but Swennen (1969) and Hulscher (1973) reported Macoma balthica crawling across the sediment and all specimens examined were found to contain gymnophallid trematode parasites (Macoma is an intermediate host and birds are the final host, Cheng 1979). It is possible that the behaviour of Spisula, Donax and Ensis is also affected by trematode infections, or they may be responding to an infaunal predator (Amphiporus lactifloreus) or physical changes in the substratum.

5.3.4 Seal predation

A herd of common seals (Phoca vitulina) was observed to occupy the nearshore bar immediately opposite the study area, particularly in August and September after the pups were born. Generally, 50-150 seals could be seen, but Bonner (1972) has pointed out that direct counts of common seals hauled out at low water are not very accurate and invariably represent an underestimate.

Common seals usually frequent estuaries and coasts, spending much of their time on sandbanks exposed at low water. Interestingly, Bonner noted that opportunities for observation in this habitat are very limited. Their habit of selecting a bank which gives immediate access to deep water channels provided an excellent opportunity for observation at Tentsmuir. The main herd was located about 500 m from an observation tower at the edge of the beach (Figure 2-2).

Casual observations and direct counts of this herd indicated that further investigation should be made on the influence of these seals on the Lanice tidal channel sub-environment. Seals are carnivores, consumers of fish mainly, although molluscs and crustaceans may form a significant part of their diet, and common seals are known to eat pleuronectids. Thus, they may have acted as an important control on the fish population in the tidal channel and possibly exploited the rich fauna of the dense Lanice association. Indeed, one seal was observed feeding or playing near the tidal channel margin of the study area in May 1978. Seals are also a potential source of lebensspurren from crawling tracks (Reineck 1959),

birth sites (the seals trample the sand in a circle around the birth site, Bonner 1972), or buried carcasses (Schäfer 1972). These traces would be signs of emergence if preserved, but their occurrence on sandbanks with high rates of reworking would limit their preservation potential.

5.4 Tube effects

The tubes of L. conchilega provided protection from polychaete predation for small Lanice in artificial enclosures. They also appeared to provide a structural refuge for other infaunal polychaetes and may have mediated the effects of disturbance by large epifaunal predators (eiders). The presence of the projecting tubes provided a substratum for attachment of epifaunal bivalves (M. edulis) which may have attracted disturbance and predation. The dense tube aggregations also seemed to attract predation from waders and some of this predation activity may have been linked with the disturbance of the substratum and exposure of infaunal species. The effects of the tubes on predation are clearly complex, perhaps best understood as the provision of structural heterogeneity in an otherwise homogeneous environment. This increased heterogeneity may lead simultaneously to increased overall predation (because of increased species richness and abundance) and increased probability of survival of individual prey (because of structural refugia). The effects of predation and disturbance are confounded by effects from the physical instability of the environment (current and wave scour) and larval settlement patterns (dependent on larval availability, hydrodynamic influences and habitat selection).

Woodin (1978) has described a similar example where the tubes of Diopatra cuprea provided structural refugia from the feeding disturbance of the blue crab, Callinectes sapidus, and the horseshoe crab, Limulus polyphemus. These crabs disrupted the surface layers of the sediments when feeding not unlike the eider activity at Tentsmuir. Dayton and Oliver (1980) stated that Van Blaricom (1978) documented infaunal colonization of similar depressions made by rays in California and fish feeding on the infauna displaced by the rays. More work is needed in highly disturbed sand environments before these complex interactions can be generalised.

Large, tube-building polychaete species are common in dynamic sand environments and appear to have important structural effects on these easily disturbed habitats (Diopatra cuprea, Woodin 1978, Brenchley 1979; Spiochaetopterus oculatus, Woodin 1978, Virnstein 1979; Phyllochaetopterus verrilli, Mesochaetopterus sagittarius, Bailey-Brock 1979; Petaloproctus socialis, Americonuphis magna, Wilson 1979; Owenia fusiformis, Fager 1964). These structural effects are not necessarily a simple stabilisation, but a more complex interaction between organisms (animals and plants), organic structures (tubes in this case), organic secretions (mucus), resultant biochemical effects from secretions and tube irrigation (Allen 1980), fluid flow and sediment particles (Eckman et al. 1981).

Organism mediated influences on sediment and community structure are of primary importance to palaeoecologists and sedimentologists as well as benthic marine ecologists. Biologically induced structural effects in cohesive sediments (mud) have been carefully investigated and it has been demonstrated that they have important biological, sedimentological and

palaeontological implications (see Rhoads 1974, 1975 and Rhoads and Boyer 1982 for reviews). It is suggested here that biologically induced structural effects in non-cohesive sediments (sand) may also have important implications for community structure, sediment transport and interpretation of preserved sedimentary sequences.

Table 5-1

Frequencies of occurrence and abundances for all infaunal species in all samples (51) from 21 localities at Tentsmuir Beach, April 1978 to October 1979.

Species	Occurrence	Abundance	
	%	Total	m^{-2}
Nephtys cirrosa	98	419	105
Tellina tenuis	90	1779	483
Lanice conchilega	78	4449	1390
Ophelia limacina	78	212	66
Eumida sanguinea	49	294	147
Harmothoë lunulata	43	49	28
Anaitides maculata	39	86	54
Spisula solida	35	39	27
Donax vittatus	29	18	15
Carcinus maenas	27	62	55
Mytilus edulis	22	391	444
Scoloplos armiger	22	15	16
Crangon crangon	20	32	40
Nephtys caeca	20	18	16
Nereis diversicolor	16	10	19
Nereis pelagica	10	9	22
Chamelea gallina	10	7	18
Amphiporus lactifloreus	10	7	18
Travisia forbesii	8	7	19
Cerastoderma edule	8	5	16
Ammodytes tobianus	6	5	21

Thracia phaseolina	4	4	25
Ensis siliqua	4	3	19
St nelais boa	4	2	13
Asterias rubens	4	2	13
Eurydice pulchra	2	2	25
Lagis koreni	2	1	13
Anaitides groenlandica	2	1	13
S pis fuliginosa	2	1	13
Magelona papill co s	2	1	13

Table 5-2

Frequencies of occurrence and average density of major infaunal species from Lanice dominated associations. Only species or genera represented at more than one location are included in this Table. The results of Buhr (1979) and Eagle (1975) were obtained from subtidal localities (boreal offshore muddy sand association of Jones 1950) and those of Ollivier (1969) from a tidal flat with abundant sea-grass (Zostera) (boreal shallow mud association & boreal shallow vegetation association of Jones 1950). The results from the present study (Carey) are presented in three groups related to Lanice tube density visible from the surface (High:>1000 tubes m^{-2}. Mod:<1000, >100 tubes m^{-2}. Low:<100 tubes m^{-2}) and are from a tidal channel margin (boreal shallow sand association of Jones 1950).

Species	Ollivier		Eagle		Buhr		Carey					
							High Tube		Mod Tube		Low Tube	
	%	m^{-2}	%	m^{-2}	%	m^{-2}	%	m^{-2}	%	m^{-2}	%	m^{-2}
Lanice conchilega	100	725	100	1770	83	4375	100	1910	100	427	39	31
Eumida sanguinea	100	56	100	1030	56	34	85	135	11	29	6	2
Anaitides spp.	80	25	100	265	39	13	62	39	16	25	6	0.7
Scoloplos armiger	80	37	63	40	50	15	19	4	11	4	22	3
Nephtys spp.	70	50	94	280	81	32	100	125	100	127	94	73
Harmothoë lunulata	80	21			69	32	81	57	5	4		
Phloë minuta			38	180	44	6						
Magelona papillicornis			75	175			4	0.5				
Nereis spp.					28	3	42	9	5	2		
Abra alba			75	110	39	17						
Veneridae	70	13			19	2	12	2			11	1

Table 5-3

Frequencies of occurrence and average density of major infaunal species from Tellina-dominated associations compared with results from all samples taken at Tentsmuir Beach. Only species or genera represented at more than one location are included in this table. The results of Stephen (1928) are from four stations at low water on the West Sands, St. Andrews (an exposed beach) in June 1928. The results of McIntyre and Eleftheriou (1968) are from four stations near mean low water spring on a beach at Firemore Bay, Loch Ewe (a relatively sheltered beach) in August and March 1965. The results of the present study are presented in three groups corresponding to Lanice tube density visible on the surface (High:>1000 tubes m^{-2}. Mod:<1000, >100 tubes m^{-2}. Low:<100 tubes m^{-2}). The present study results (Carey) are from mean low water spring on a tidal channel margin at Tentsmuir Beach in April, May, July, August, and October 1978 and March 1979.

All of these localities are within the boreal shallow sand association of Jones (1950).

	Stephen		McIntyre & Eleftheriou		Carey					
					High tube		Mod tube		Low tube	
	%	m^{-2}	%	m^{-2}	%	m^{-2}	%	m^{-2}	%	m^{-2}
Tellina tenuis	100	1072	100	128	100	610	100	482	72	181
Donax vittatus	100	457			31	4	11	5	5	3
Nephtys spp.	100	44	88	22	100	125	100	127	94	73
Nerine spp.	25	6	100	41						
Scolelepis fuliginosa	25	2							6	1
Magelona papillicornis	25	1	4	2	4	1				

Table 5-4

Abundances of all infaunal species from four samples collected during a transplantation experiment in 1979. Two samples (LTC1 and LTC2) were collected adjacent to the transplant plot before the transplantation began in April 1979. The transplantplot (40 cm x 100 cm) was seeded with 0.5 L. conchilega cm^{-2} in April 1979 and the sample (LTT1) was collected in October 1979. The surface of the control plot (40 cm x 100 cm) was disturbed to a depth of 2 cm in April 1979 and the sample (LTC3) was collected in October 1979. All samples were washed through a 0.5 mm mesh nylon sieve and collected with 4 can-cores (0.08 m^2).

	April Before control LTC 1	April Transplant control LTC 2	Oct After control LTC 3	Oct Transplant transplant LTT 1
Nephtys cirrosa	12	10	13	15
Tellina tenuis	40	28	47	12
Lanice conchilega	4	15	9	77
Ophelia limacina	11	0	5	1
Eumida sanguinea	0	3	0	7
Harmothoë lumulata	0	0	0	0
Anaitides maculata	0	7	0	10
Spisula solida	0	0	1	0
Donax vittatus	0	0	1	1
Scoloplos armiger	0	0	1	2
Mytilus edulis	467	135	0	150
Crangon crangon	0	0	0	15
Nephtys caeca	p	1	0	0
Amphiporus lactifloreus	1	0	0	0

Asterias rubens	0	0	0	1
Total abundance	535	199	77	291
Total abundance (without *M. edulis*)	68	64	77	141

Table 5-5

Incidence of attachment of juvenile tubes (<2 mm. in diameter) of L. conchilega in a transplantation experiment. Both samples were collected in October 1979 and represent 0.08 m^{-2}. The transplant sample was seeded with 0.5 L. conchilega cm^{-2} in April 1979 and the surface of the control was disturbed in April 1979. Size class data for all L. conchilega in each sample are given at the bottom of the Table. Adults >1 year were all those worms with tubes >2 mm in diameter; young <1 year were all those worms with tubes > 1 mm, <2 mm in diameter; juveniles (newly settled) were all those worms with tubes <1 mm in diameter.

Tubes with attached juvenile tubes	Transplant sample LTT 1	control sampl LTC 3
Occupied adult Lanicetubes	4	0
Occupied attached juvenile tubes	5	0
Occupied adult Lanice tubes	4	0
Unoccupied attached juvenile tubes	4	0
Unoccupied adult Lanice tubes	4	3
Occupied attached juvenile tubes	6	3
Unoccupied adult Lanice tubes	7	5
Unoccupied attached juvenile tubes	11	9
Totals		
adult tubes[1]	17	7
juvenile tubes	26	12
adults	7	0
juveniles	11	3
All Lanice conchilega		
Adults > 1 year	25	2
Young < 1 year	27	4
Juveniles (newly settled)	25	3
Totals	77	9

1. Some adult tubes had both occupied and unoccupied juvenile tubes attached and are recorded in two categories.

Table 5-6

Abundances of all infaunal species from two samples collected after browsing activity of Eider ducks in March 1979. One sample (EBT 1) was collected from the centre of an Eider browsing trace 0.5 m in diameter. The other sample was collected 0.5 m from the centre of the trace. Both samples were collected with 4 can-cores (0.08 m^2) from the same algal-Lanice mound and washed through a 0.5 mm mesh nylon sieve.

	INSIDE EIDER BROWSING TRACE EBT 1	OUTSIDE EIDER BROWSING TRACE EBT 2
Nephtys cirrosa	11	9
Tellina tenuis	41	53
Lanice conchilega	163	198
Ophelia limacina	0	3
Eumida sanguinea	9	8
Harmothoë lunulata	2	3
Anaitides maculata	5	12
Donax vittatus	0	1
Spisula solida	1	0
Carcinus maenas	0	22
Mytilus edulis	9	65
Chamelea gallina	0	2
Cerastoderma edule	0	1
Total abundance	241	377
Total abundance without M. edulis and C. maenas	232	290
Number of species	8	12

Table 5-7

Results of an enclosure experiment to investigate possible interactions between Lanice conchilega and the associated carnivorous polychaetes Anaitides maculata and Eumida sanguinea. Each pairing of species was placed in a plastic plankton holder (0.1 mm mesh) and floated on a seawater table in continuously running seawater for 65 days (14 November 1979 - 17 January 1980). Lanice were removed from their tubes (all young Lanice, mean tube diameter 2.1 mm, range 1.4 - 2.7 mm) and placed in holders. One group (with tube material) was provided with 2g of shell debris, all Lanice but one in this group built tubes and survived. The other group were not provided with shell debris and only those without predators survived, all Lanice in this group built mucous and detritus tubes.

	Lanice with tube material	Lanice without tube material	No Lanice
1 Anaitides	0, 0, 0[a]	1, 1, 1[a]	0, 0
2 Anaitides	0	1	
1 Eumida	0	1	
No predator	0, X[b]	0, 0	

1= interaction, prey species (Lanice) dead, predator alive

0= no interaction, both species alive

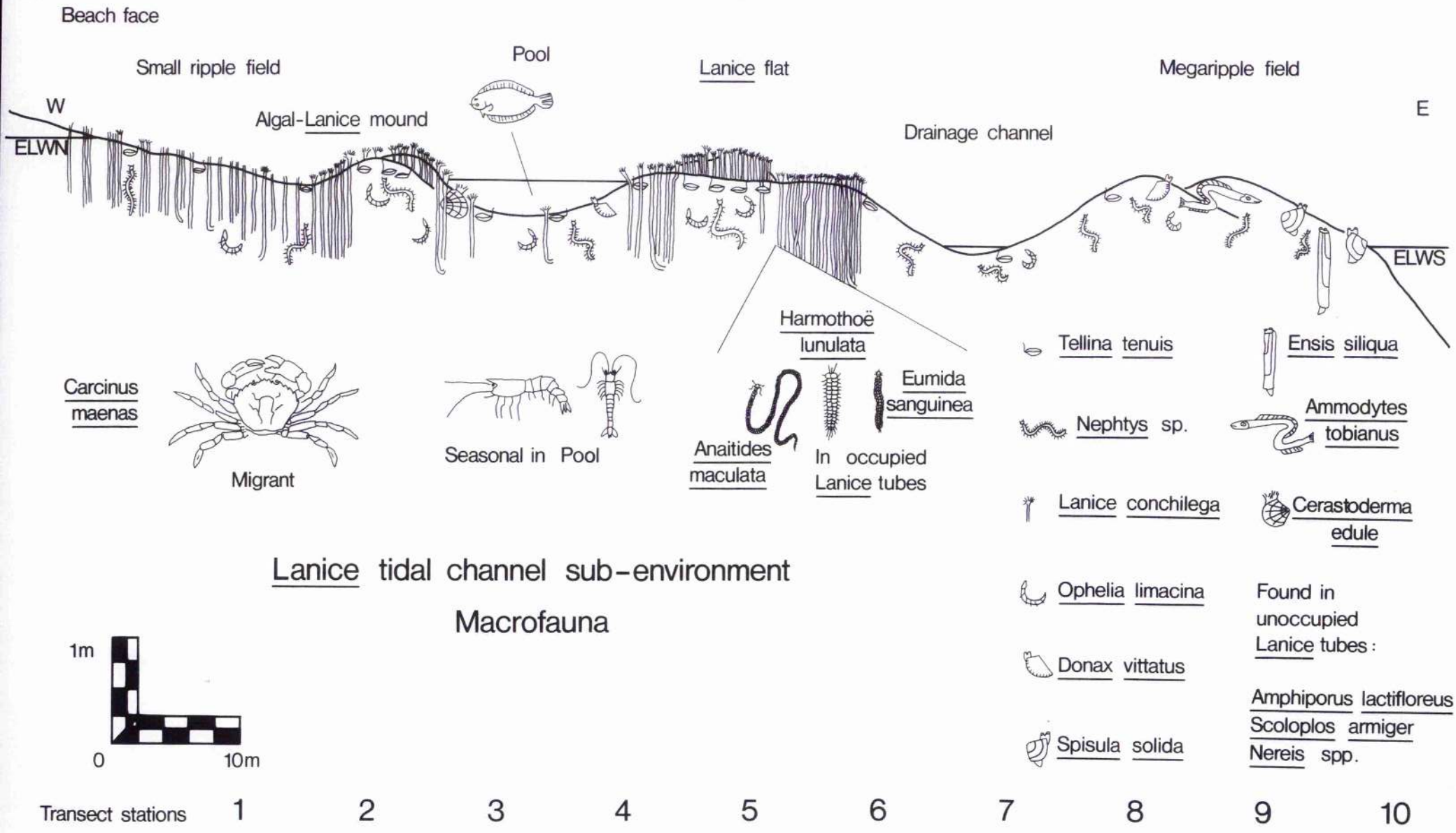
X= both species dead

a= Sample contained 2 Lanice.

b= Sample contaminated with Leptostracan (Nebalia bipes).

Figure 5-1

The distribution of species and field divisions of the Lanice Tidal channel sub-environment at Tentsmuir Beach from May to September 1978. Animals are not drawn to scale.



Lanice tidal channel sub-environment

Macrofauna

Figure 5-2

The total abundance of all macroinfaunal species along the transect in May, August and October 1978 and March 1979

TOTAL ABUNDANCE

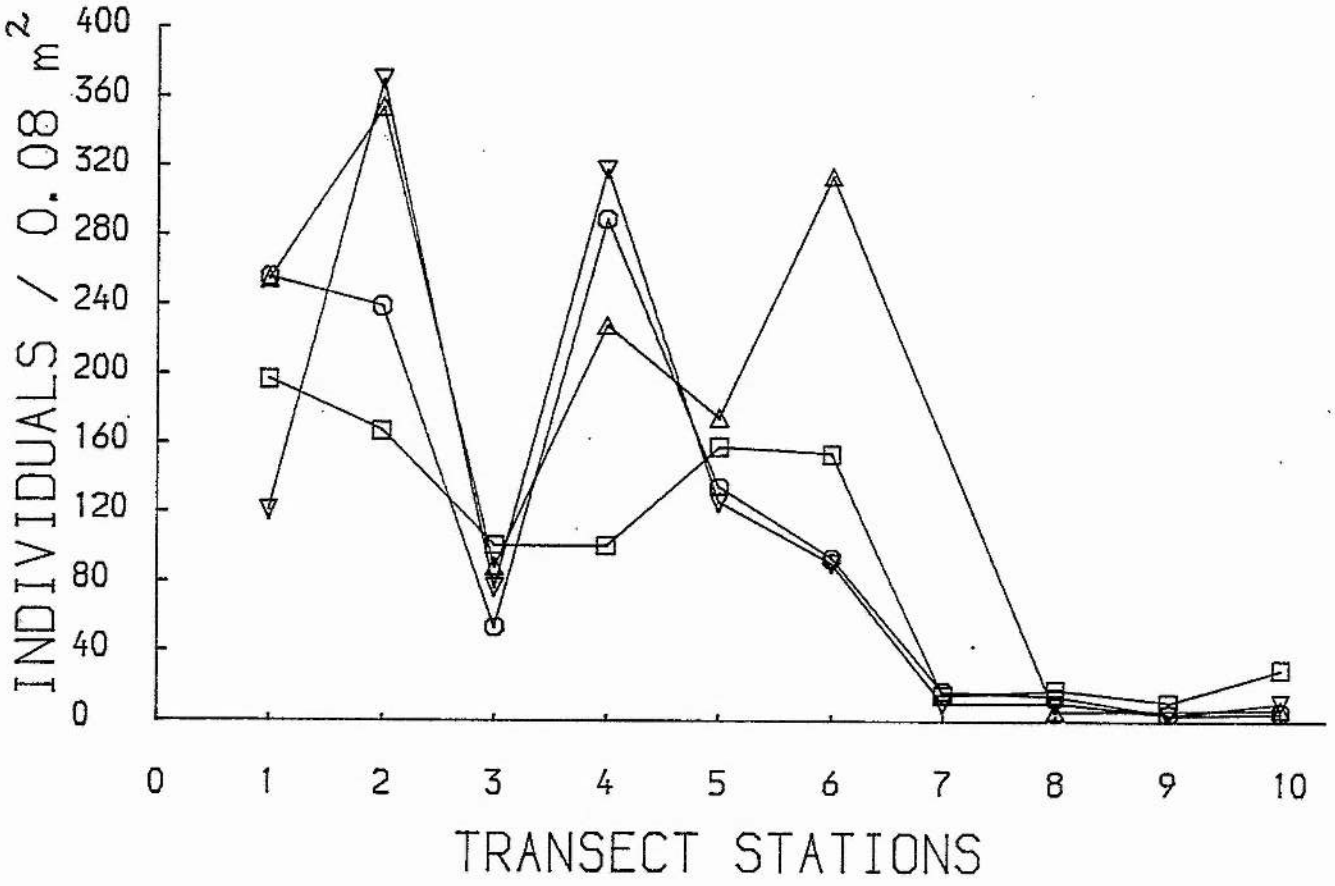


Figure 5-3

The total abundance of all macroinfaunal species except *Lanice conchilega* along the transect in May, August and October 1978 and March 1979.

TOTAL ABUNDANCE W/O LANICE

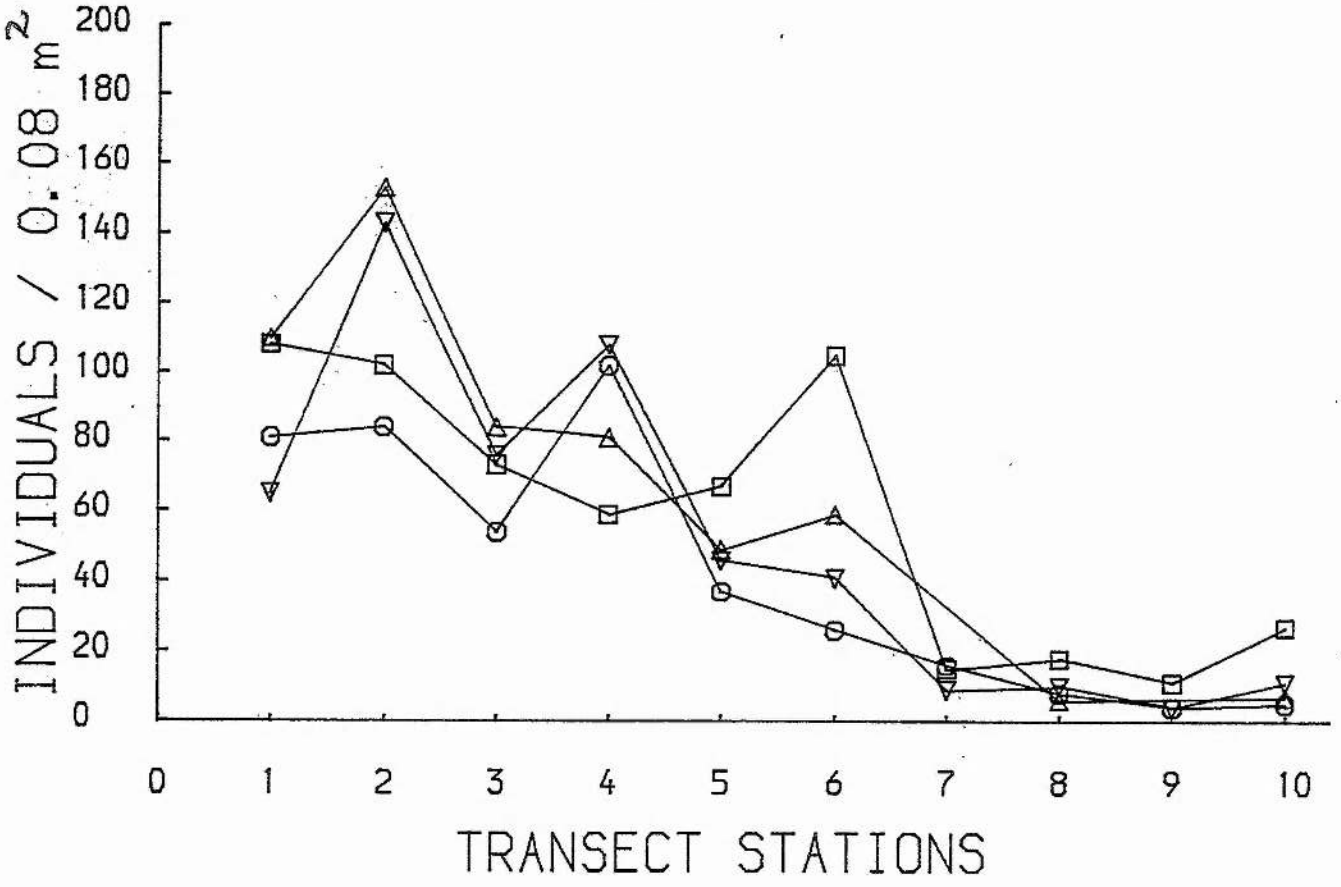


Figure 5-4

Species richness (number macroinfaunal species in each $0.08m^2$ sample) along the transect in May, August and October 1978 and March 1979.

NUMBER OF SPECIES

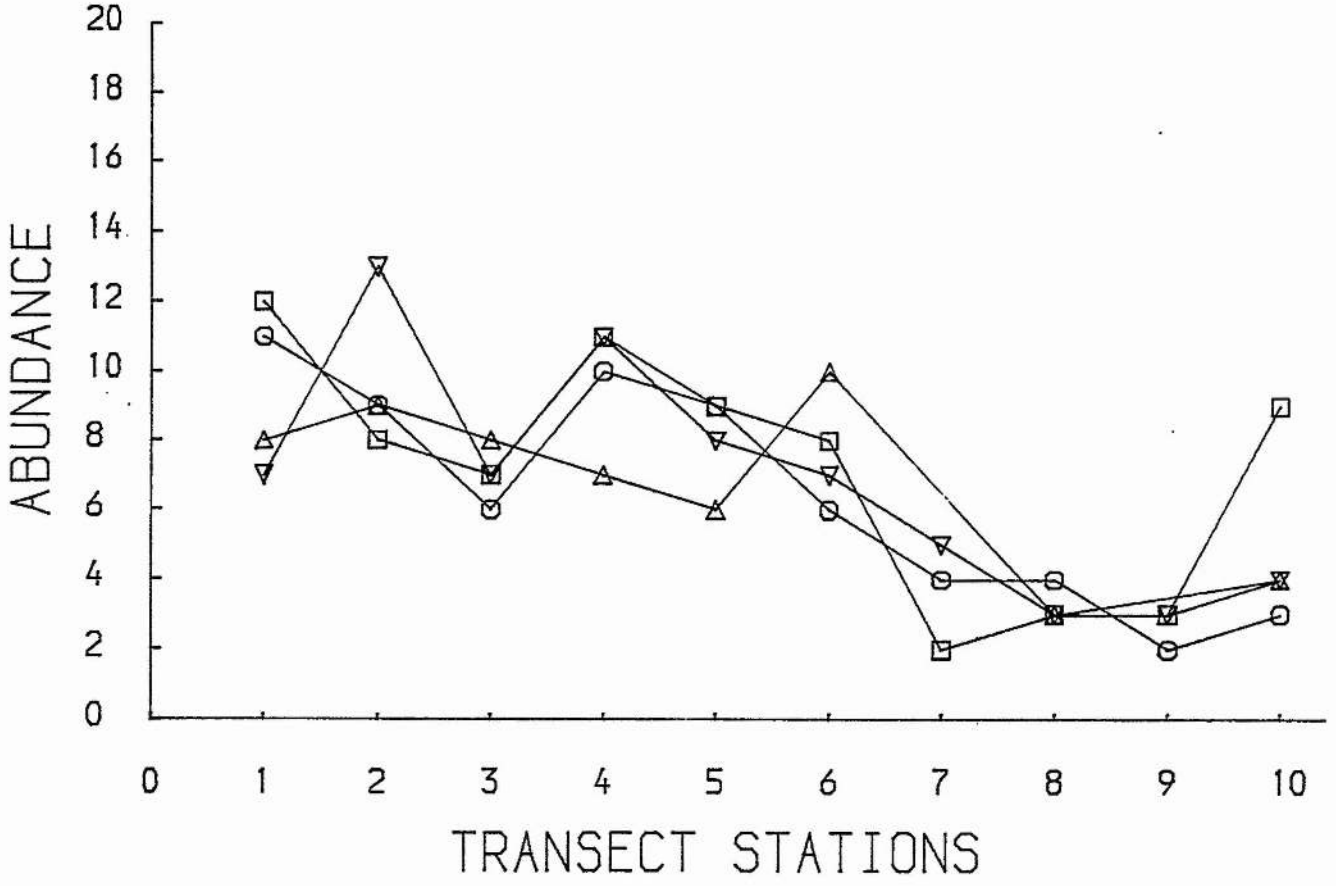


Figure 5-5

Biomass values in grams of ash-free dry weight of soft tissues. Values presented are for all macroinfauna (Total Biomass), Lanice conchilega only (Lanice Biomass), all polychaetes except Lanice (Polychaete Biomass) and all bivalves (Bivalve Biomass).

The values were obtained from $0.08m^2$ cores taken at each transect station in May 1978. Details of measurement are in Appendix II and values for individual species are in Appendix Table III.

BIOMASS MAY 1978

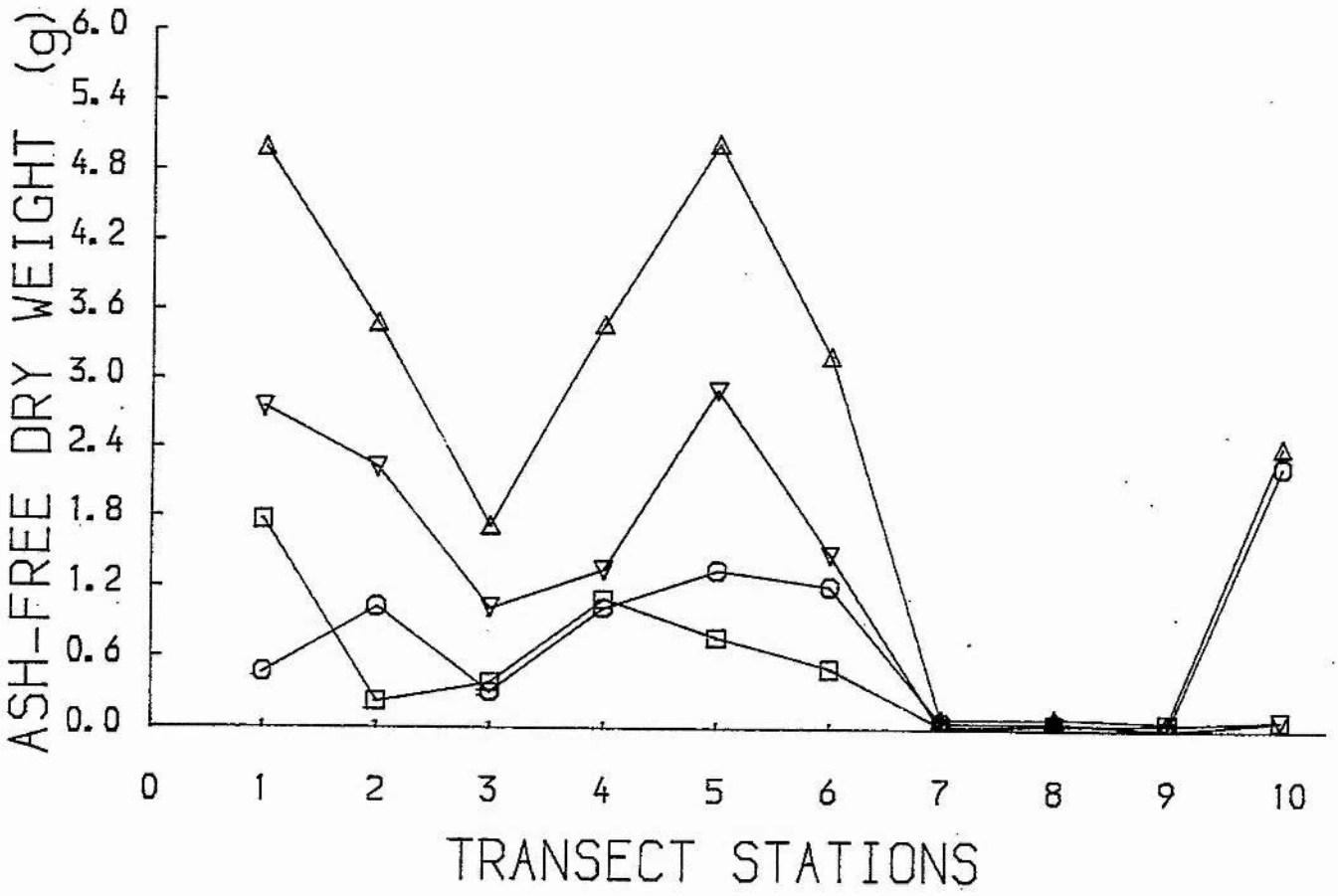


Figure 5-6

Total macroinfaunal abundance alone the transect in May 1978 with Lanice conchilega and without L. conchilega. Transect stations are numbered from 1-10 along the abscissa (horizontal axis) from left to right (see Figure 5-5). In this diagram the stations are classified into environmental divisions based on observations of the surface exposed in May 1978.

Divisions

B Beach face

R Small ripple field

A-M Algal-Lanice mound

L-F Lanice flat

P Pool

D-C Drainage channel

M-R Megaripple field

I Islet

ABUNDANCE MAY 1978

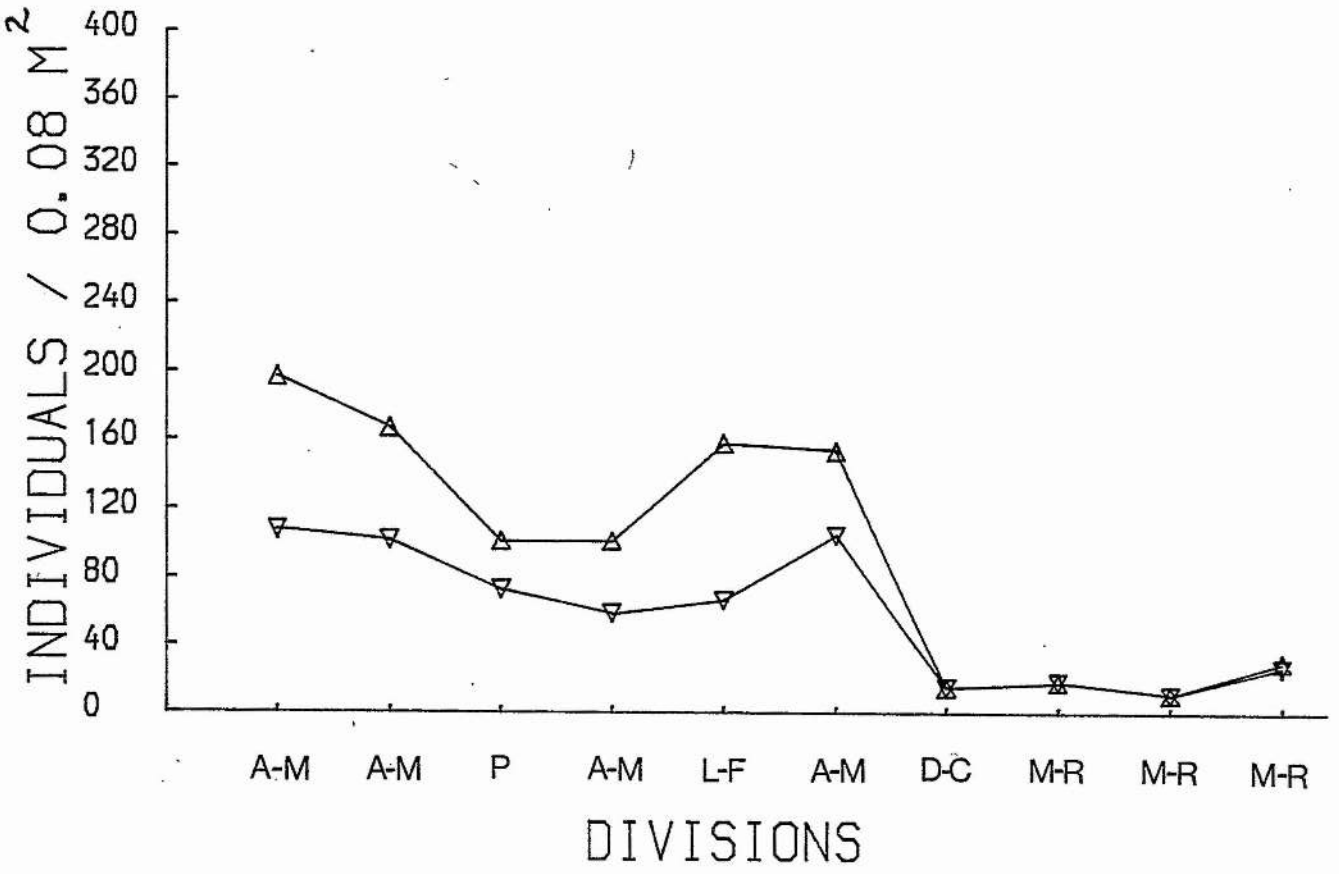


Figure 5-7

Distribution of the abundance of the seven most common species along the transect in May 1978. The abundances of *Nephtys* spp. and *Ophelia limacina* were combined in one plot and the abundances of *Eumida sanguinea* (ES), *Harmothoë lunulata* (HL) and *Anaitides maculata* (AM) were combined in another plot to allow the use of one abundance scale (see Appendix Table I for individual values).

Divisions

B Beach face

R Small ripple field

A-M Algal-*Lanice* mound

L-F *Lanice* flat

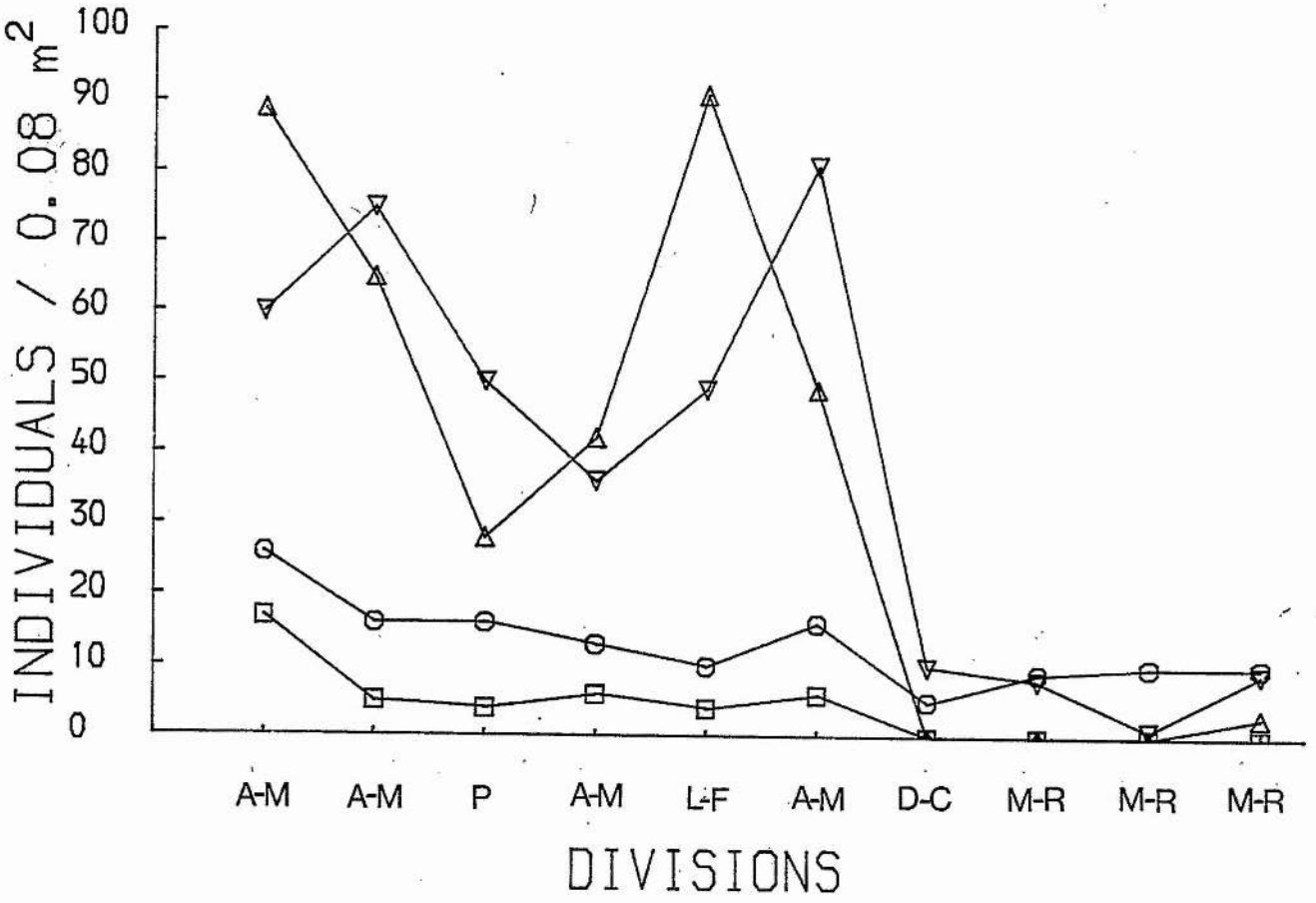
P Pool

D-C Drainage channel

M-R Megaripple field

I Islet

DISTRIBUTION MAY 1978



△ LANICE CONCHILEGA

▽ TELLINA TENUIS

○ NEPHTYS + OPHELIA

□ ES + HL + AM

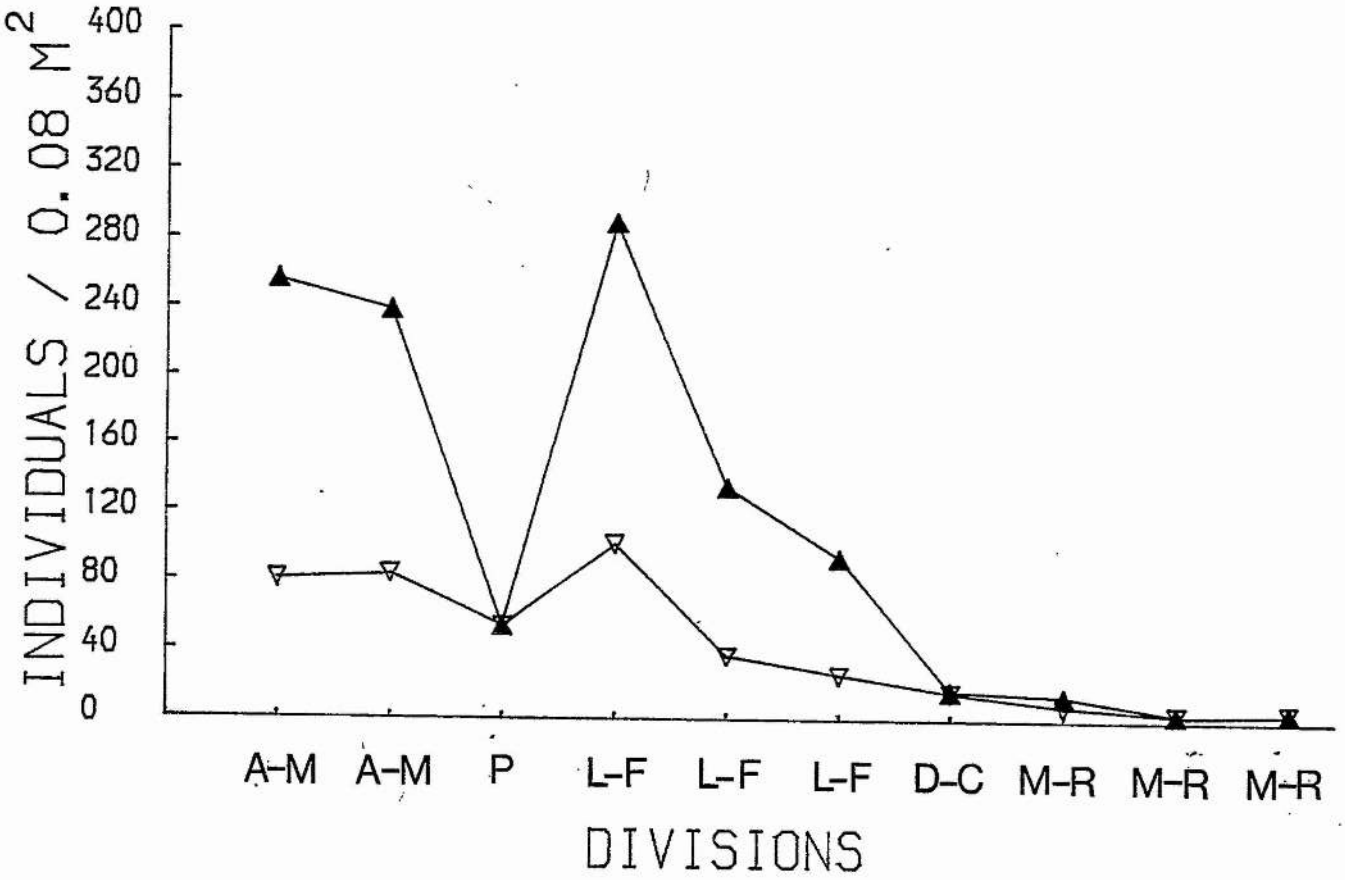
Figure 5-8

Total macroinfaunal abundance alont the transect in August 1978 with Lanice conchilega and without L. conchilega. Transect stations are numbered from 1-10 along the abscissa from left to right (see Figure 5-5). In this diagram the stations are classified into environmental divisions based on observations of the surface exposed in August 1978.

Divisions

B	Beach face
R	Small ripple field
A-M	Algal-Lanice mound
L-F	Lanice flat
P	Pool
D-C	Drainage channel
M-R	Megaripple field
I	Islet

ABUNDANCE AUGUST 1978



▲ TOTAL W/LANICE

▽ TOTAL W/O LANICE

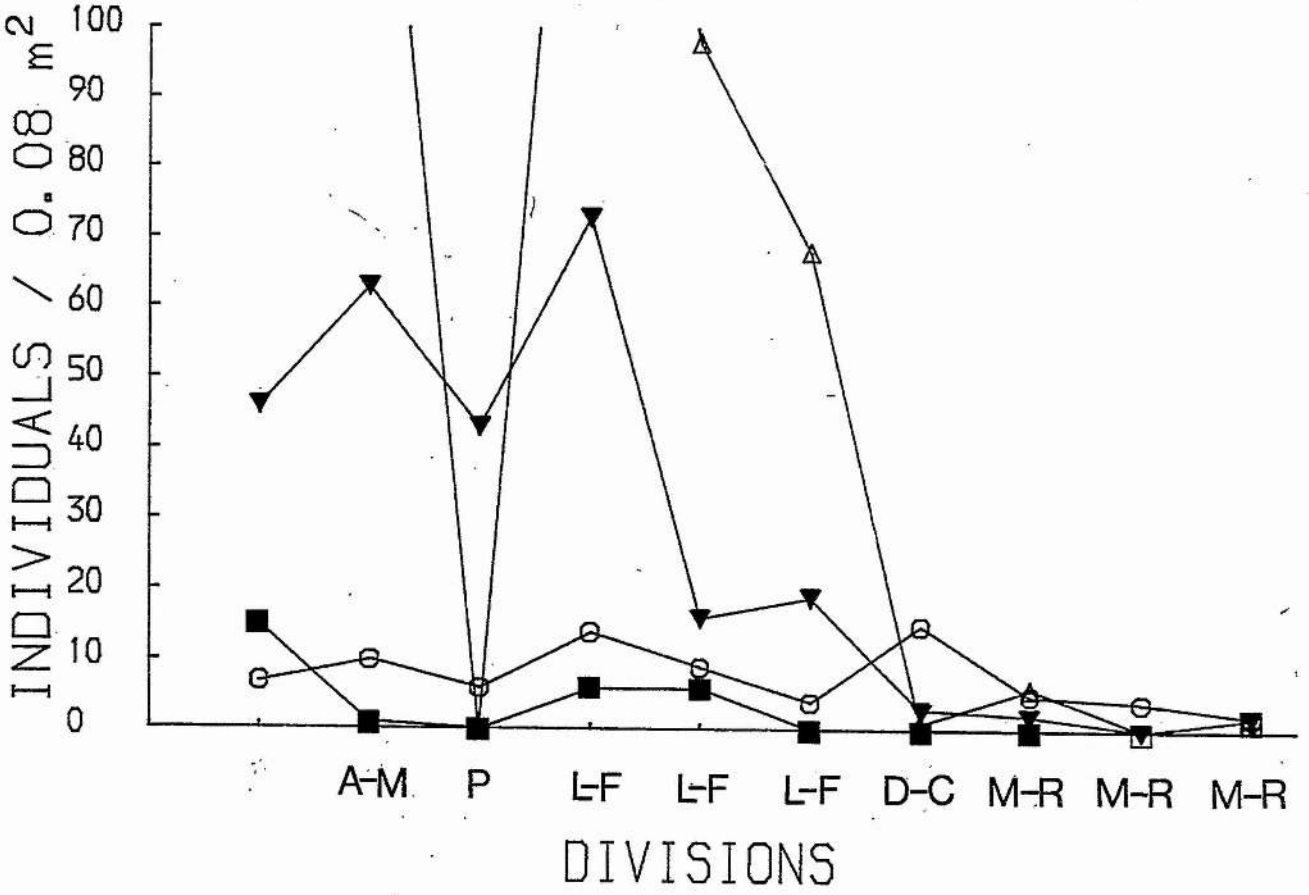
Figure 5-9

Distribution of the abundance of the seven most common species along the transect in August 1978. The abundances of *Nephtys* sp. and *Ophelia limacina* were combined in one plot, the abundances of *Eumida sanguinea* (ES), *Harmothoë lunulata* (HC) and *Anaitides maculata* (AM) were combined in another and the *Lanice conchilega* abundance extrapolated off the graph to allow the use of one abundance scale and facilitate comparison (see Appendix Table I for individual values and Figure 5-16 for plot of *Lanice* abundance).

Divisions

B	Beach face
R	Small ripple field
A-M	Algal-*Lanice* mound
L-F	*Lanice* flat
P	Pool
D-C	Drainage channel
M-R	Megaripple field
I	Islet

DISTRIBUTION AUGUST 1978



△ LANICE CONCHILEGA

▼ TELLINA TENUIS

o NEPHTYS + OPHELIA

■ ES + HL + AM

Figure 5-10

Total macroinfaunal abundance along the transect in October 1978 with Lanice conchilega and without L. conchilega. Transect stations are numbered from 1-10 along the abscissa (horizontal axis) from left to right (see Figure 5-5). In this diagram the stations are classified into environmental divisions based on observations of the surface exposed in October 1978.

Divisions

B	Beach face
R	Small ripple field
A-M	Algal-Lanice mound
L-F	Lanice flat
P	Pool
D-C	Drainage channel
M-R	Megaripple field
I	Islet

ABUNDANCE OCTOBER 1978

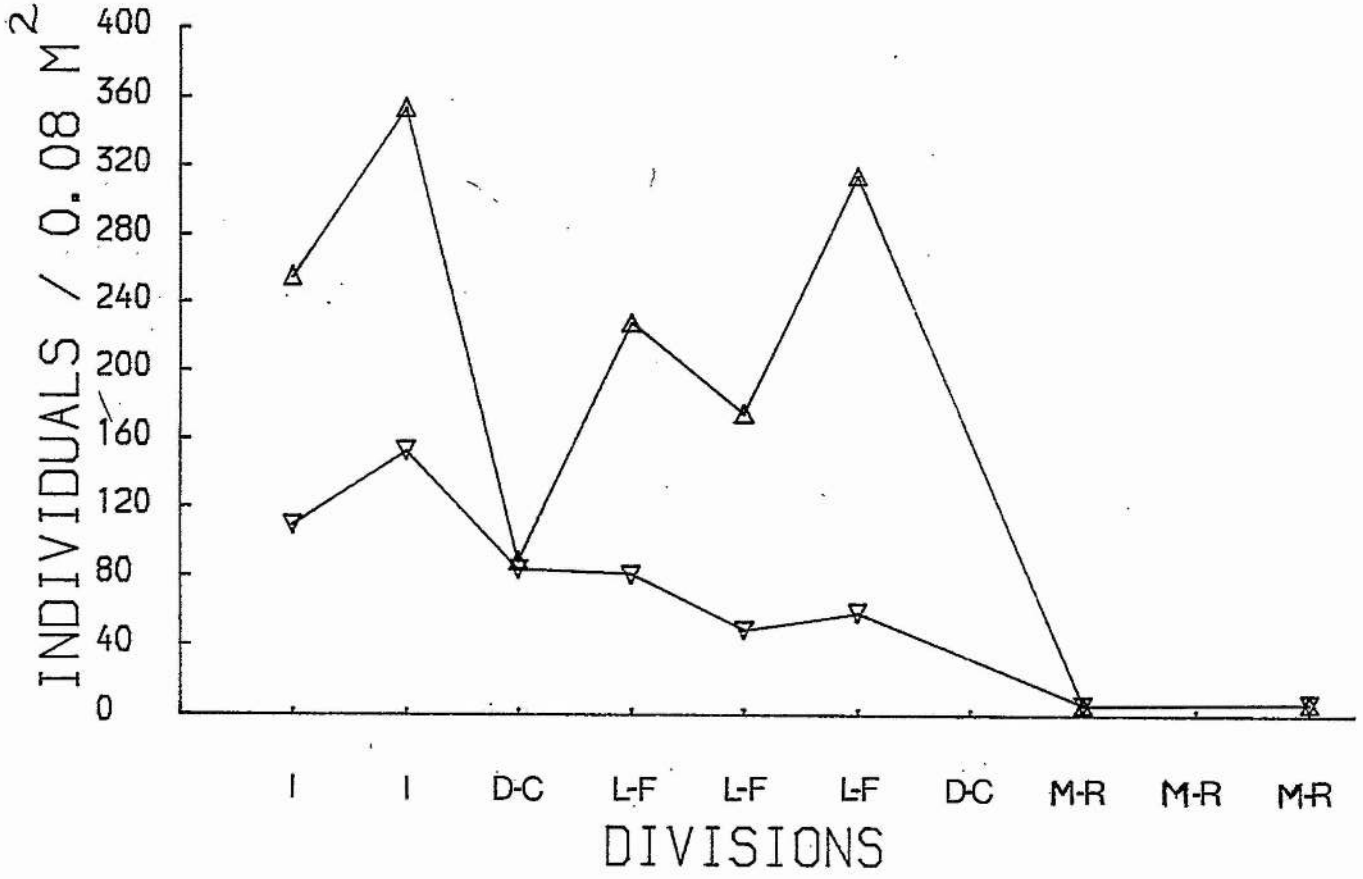


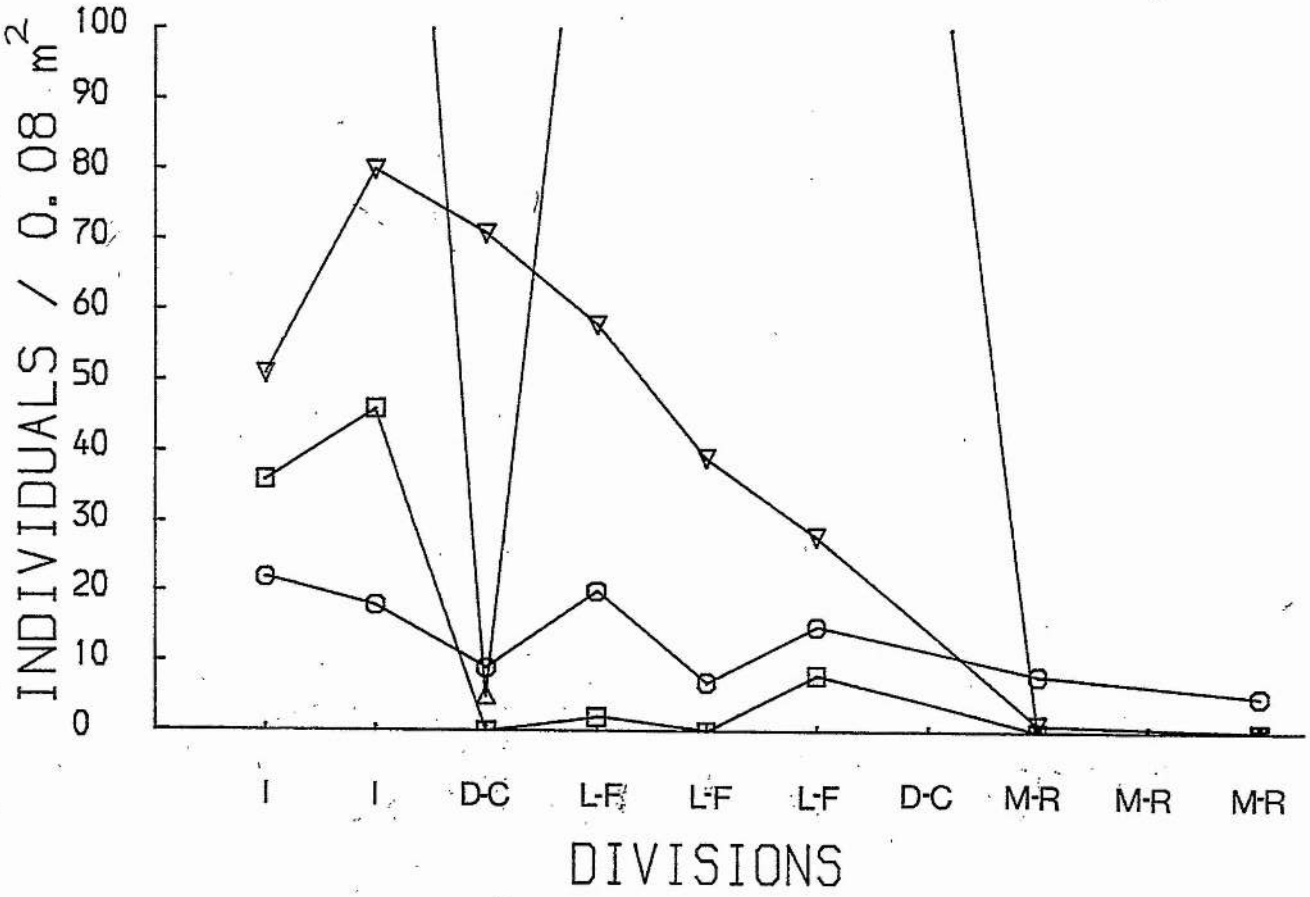
Figure 5-11

Distribution of the abundance of the seven most common species along the transect in October 1978. The abundances of Nephtys sp. and Ophelia limacina were combined in one plot, the abundances of Eumida sanguinea (ES), Harmothoë lunulata (HC) and Anaitides maculata (AM) were combined in another and the Lanice conchilega abundance extrapolated off the graph to allow the use of one abundance scale and facilitate comparison (see Appendix Table I for individual values and Figure 5-16 for plot of Lanice abundance).

Divisions

B	Beach face
R	Small ripple field
A-M	Algal-Lanice mound
L-F	Lanice flat
P	Pool
D-C	Drainage channel
M-R	Megaripple field
I	Islet

DISTRIBUTION OCTOBER 1978



△ LANICE CONCHILEGA

▽ TELLINA TENUIS

○ NEPHTYS + OPHELIA

□ ES + HL + AM

Figure 5-12

Total macroinfaunal abundance alone the transect in March 1979 with Lanice conchilega and without L. conchilega. Transect stations are numbered from 1-10 along the abscissa (horizontal axis) from left to right (see Figure 5-5). In this diagram the stations are classified into environmental divisions based on observations of the surface exposed in March 1979.

Divisions

B Beach face

R Small ripple field

A-M Algal-Lanice mound

L-F Lanice flat

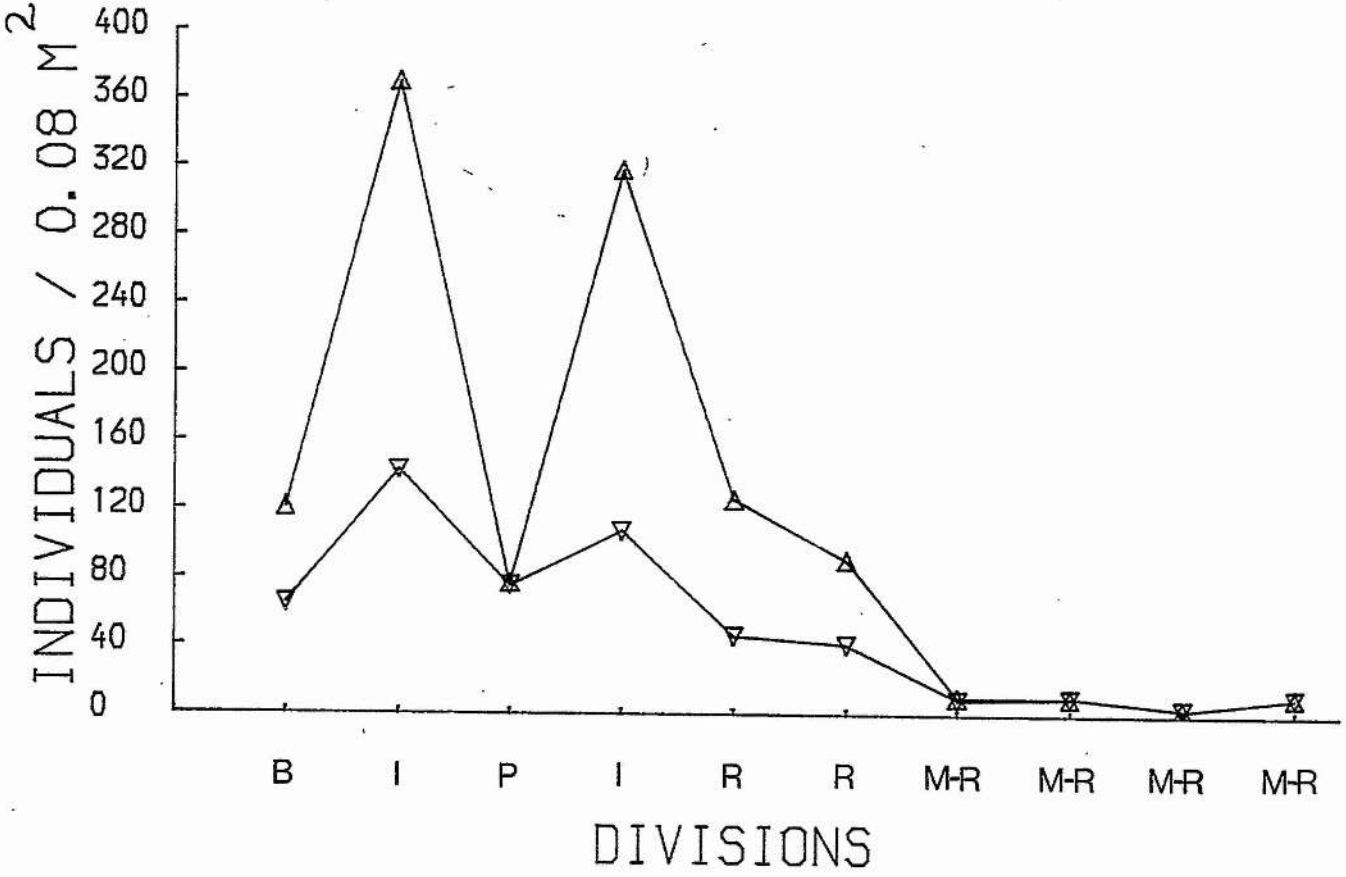
P Pool

D-C Drainage channel

M-R Megaripple field

I Islet

ABUNDANCE MARCH 1979



△ TOTAL W/LANICE

▽ TOTAL W/O LANICE

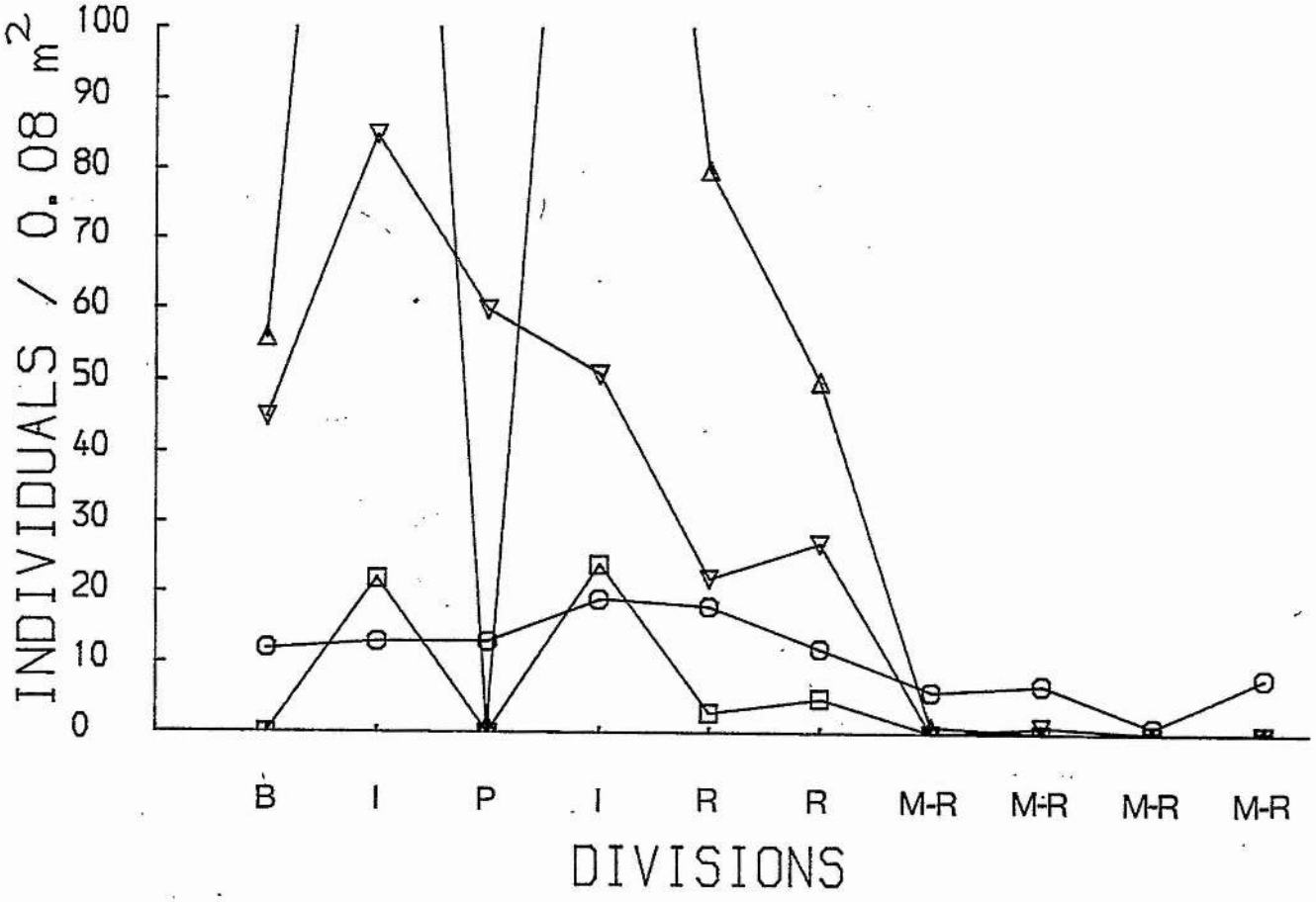
Figure 5-13

Distribution of the abundance of the seven most common species along the transect in March 1979. The abundances of *Nephtys* sp. and *Ophelia limacina* were combined in one plot, the abundances of *Eumida sanguinea* (ES), *Harmothoë lunulata* (HC) and *Anaitides maculata* (AM) were combined in another and the *Lanice conchilega* abundance extrapolated off the graph to allow the use of one abundance scale and facilitate comparison (see Appendix Table I for individual values and Figure 5-16 for plot of *Lanice* abundance).

Divisions

B	Beach face
R	Small ripple field
A-M	Algal-*Lanice* mound
L-F	*Lanice* flat
P	Pool
D-C	Drainage channel
M-R	Megaripple field
I	Islet

DISTRIBUTION MARCH 1979



△ LANICE CONCHILEGA □ ES + HL + AM

▽ TELLINA TENUIS

○ NEPHTYS + OPHELIA

Figure 5-14

Abundance of Nephtys cirrosa along the transect in May, August and October 1978 and March 1979.

NEPHTYS ABUNDANCE

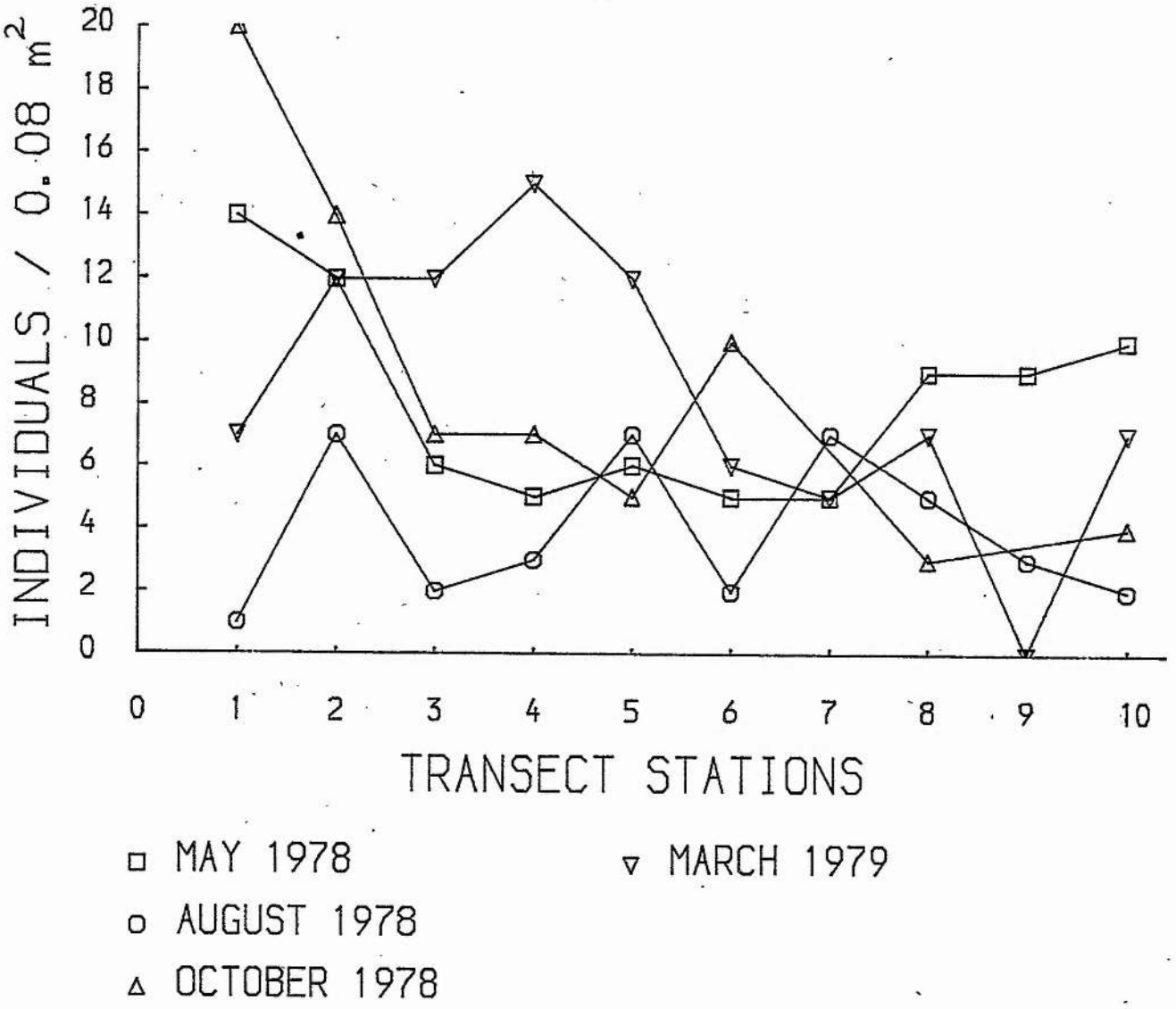


Figure 5-15

Abundance of Tellina tenuis along the transect in May, August and October 1978 and March 1979.

TELLINA ABUNDANCE

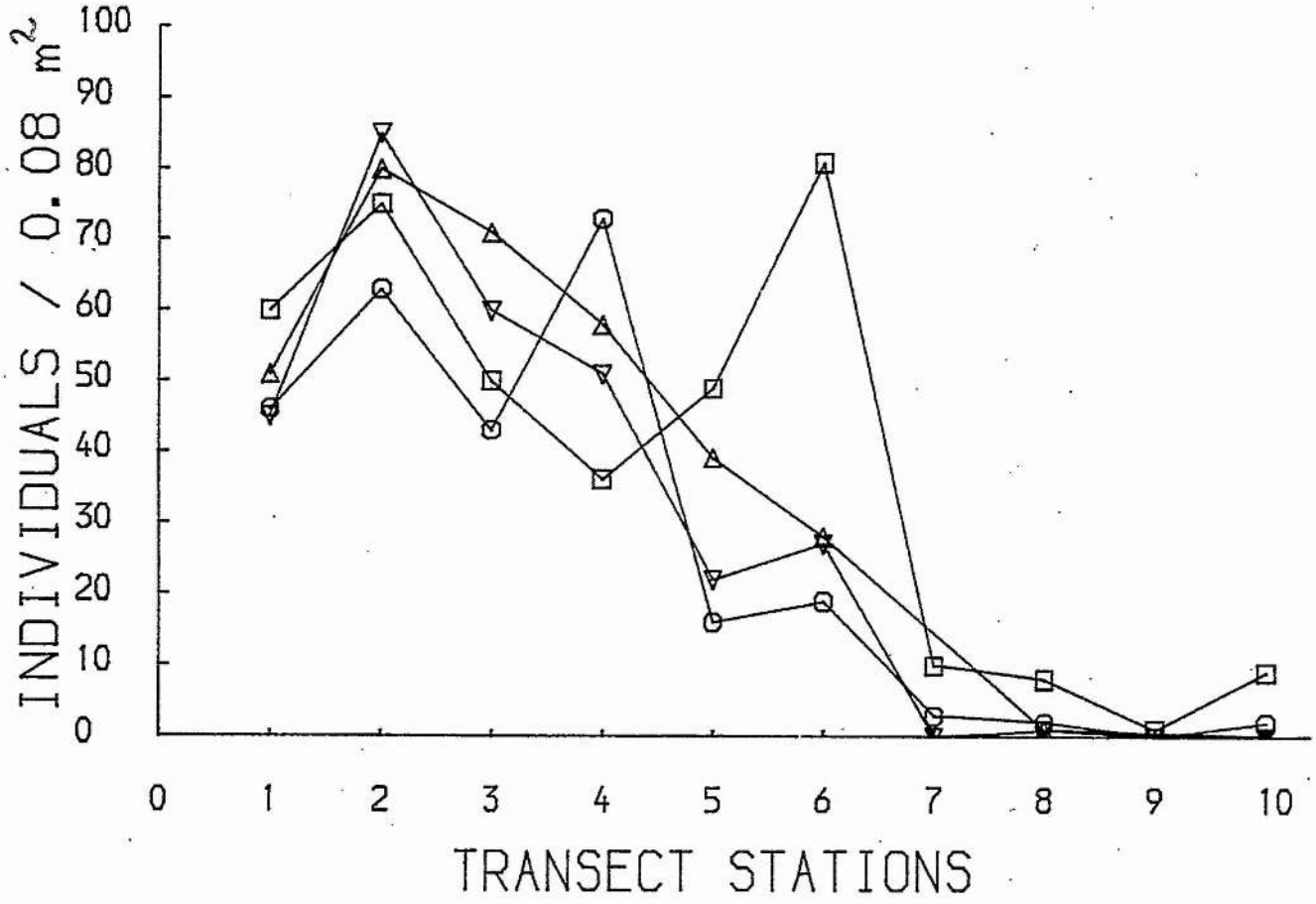


Figure 5-16

Abundance of Lanice conchilega along the transect in May, August and October 1978 and March 1979.

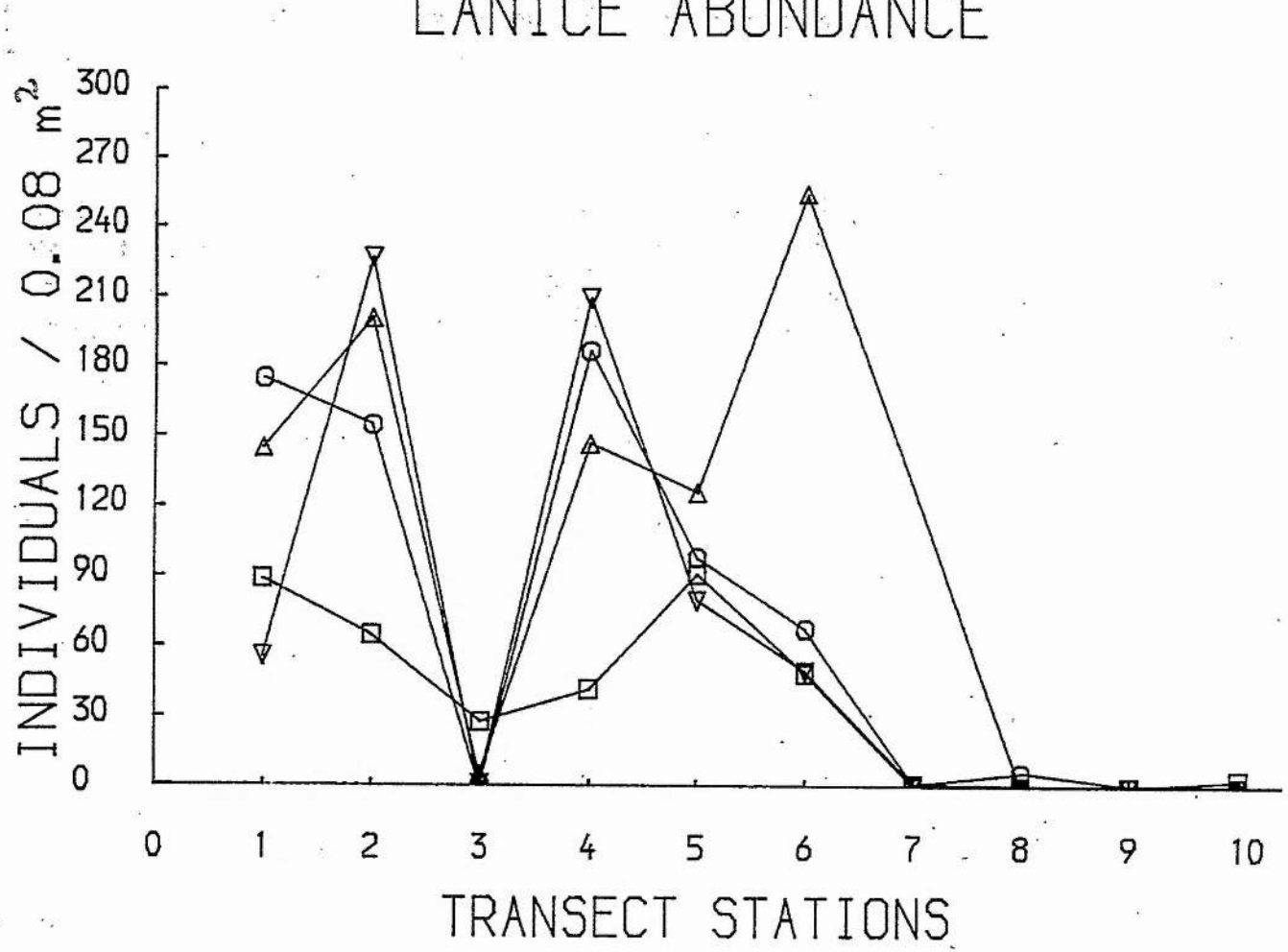

LANICE ABUNDANCE
INDIVIDUALS / 0.08 m²
300
270
240
210
180
150
120
90
60
30
0
0
1
2
3
4
5
6
7
8
9
10
TRANSECT STATIONS
MAY 1978
AUGUST 1978
OCTOBER 1978
MARCH 1979

Figure 5-17

Abundance of Ophelia limacina along the transect in May, August and October 1978 and March 1979.

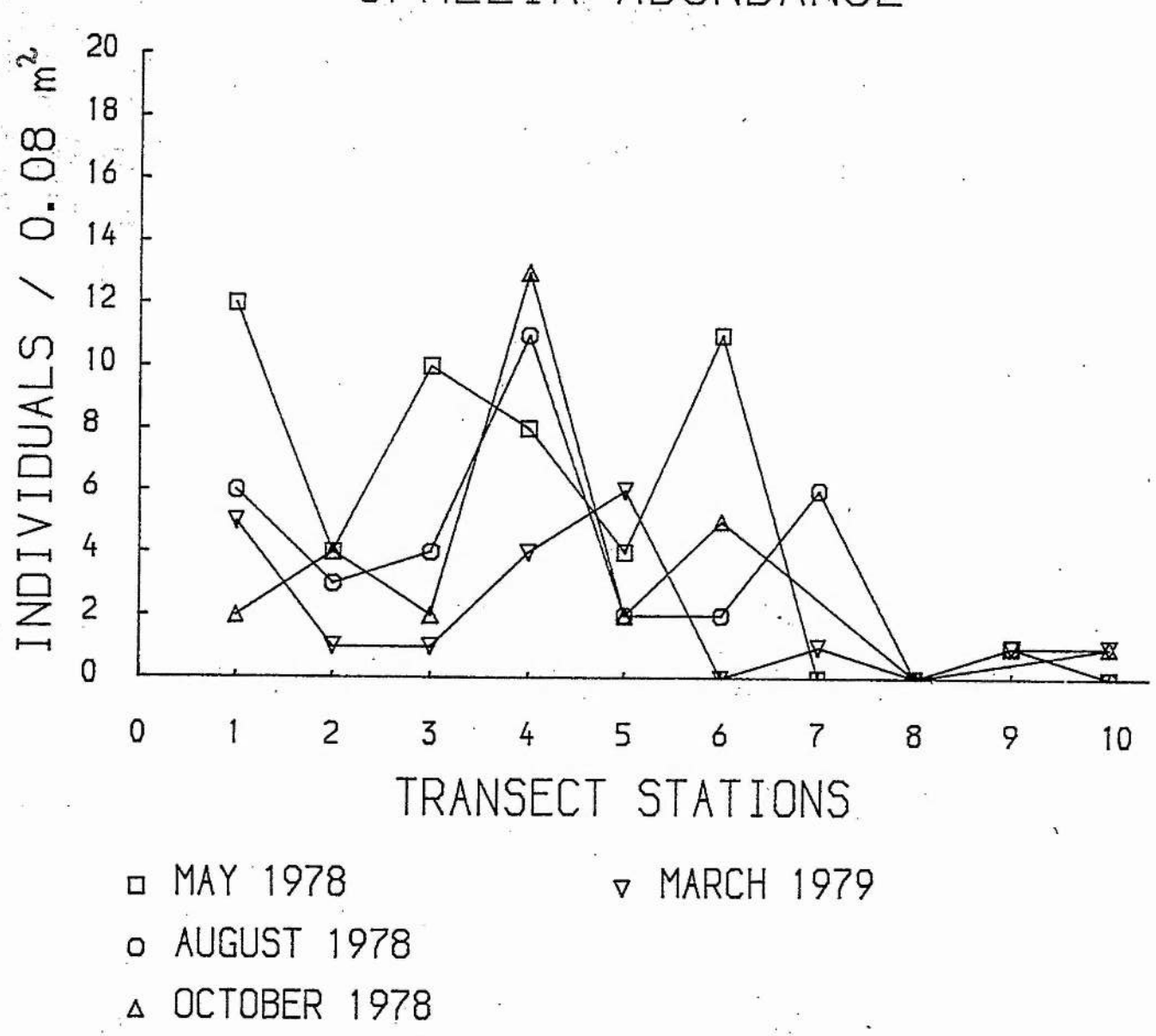

OPHELIA ABUNDANCE
INDIVIDUALS / 0.08 m²
20
18
16
14
12
10
8
6
4
2
0
0
1
2
3
4
5
6
7
8
9
10
TRANSECT STATIONS
MAY 1978
AUGUST 1978
OCTOBER 1978
MARCH 1979

Figure 5-18

Abundance of Eumida sanguinea along the transect in May, August and October 1978 and March 1979.

EUMIDA ABUNDANCE

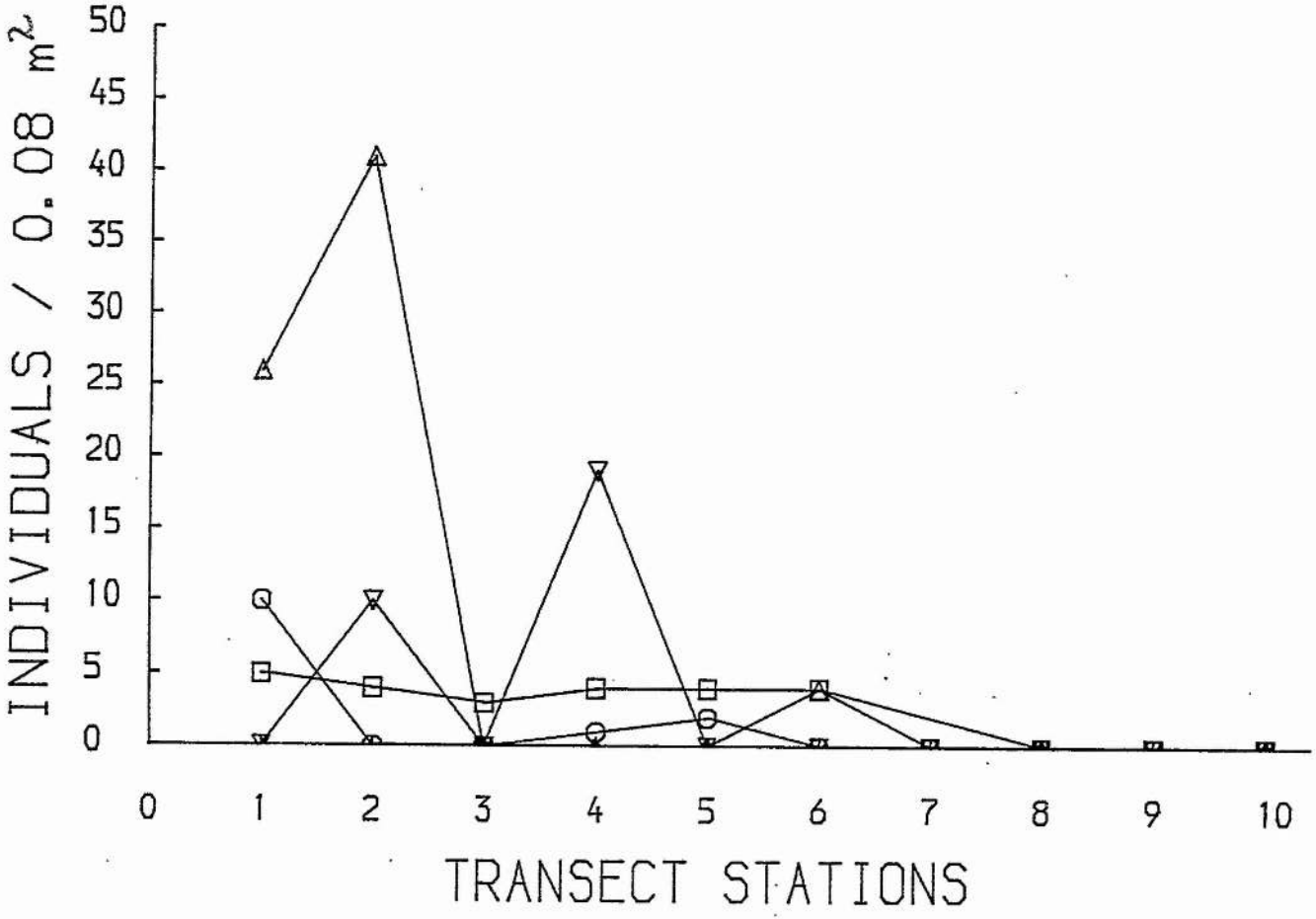


Figure 5-19

Abundance of Harmothoë lunulata along the transect in May, August and October 1978 and March 1979.

HARMOTHOË ABUNDANCE

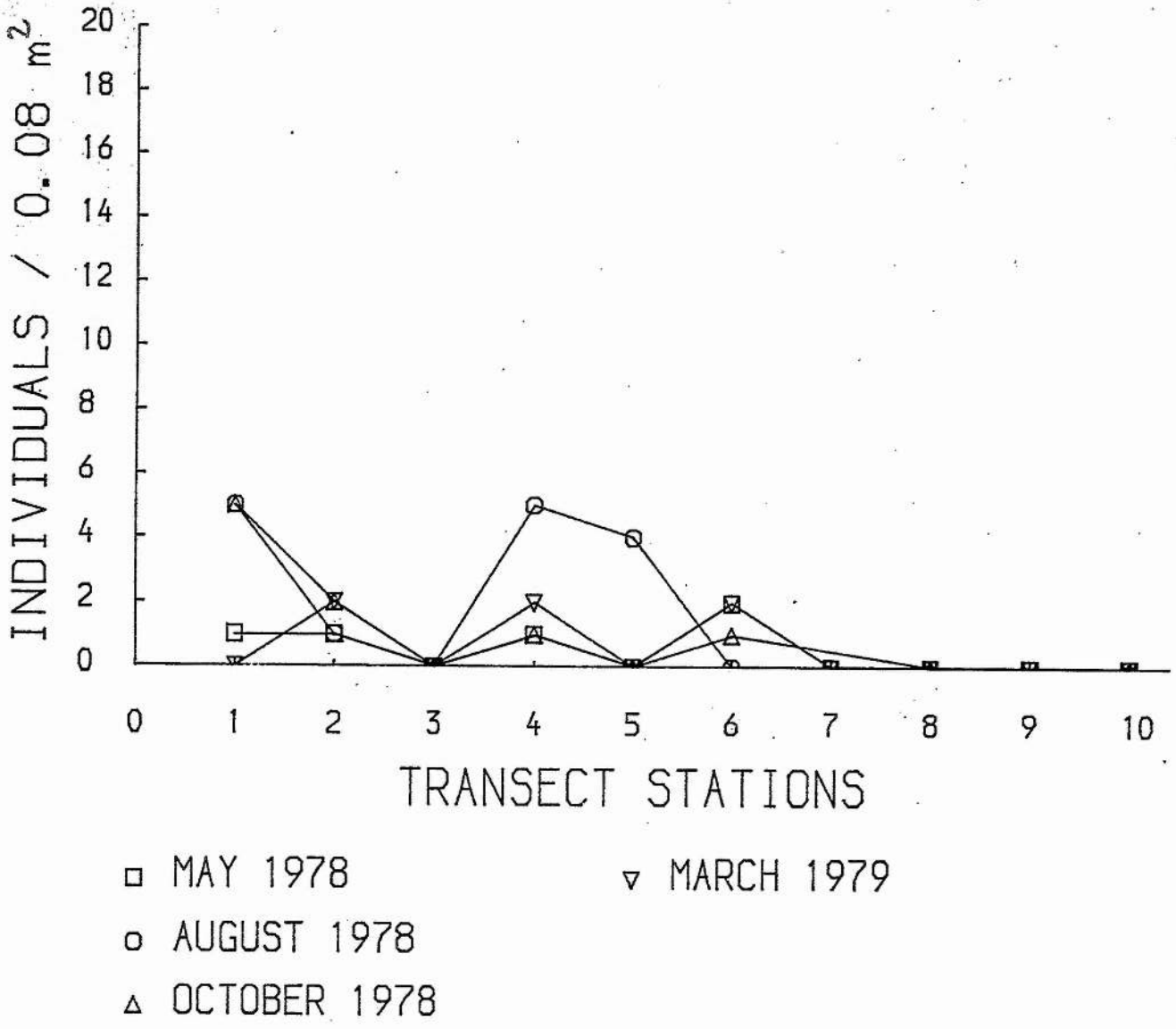


Figure 5-20

Abundance of Anaitides maculata along the transect in May, August and October 1978 and March 1979.

ANAITIDES ABUNDANCE

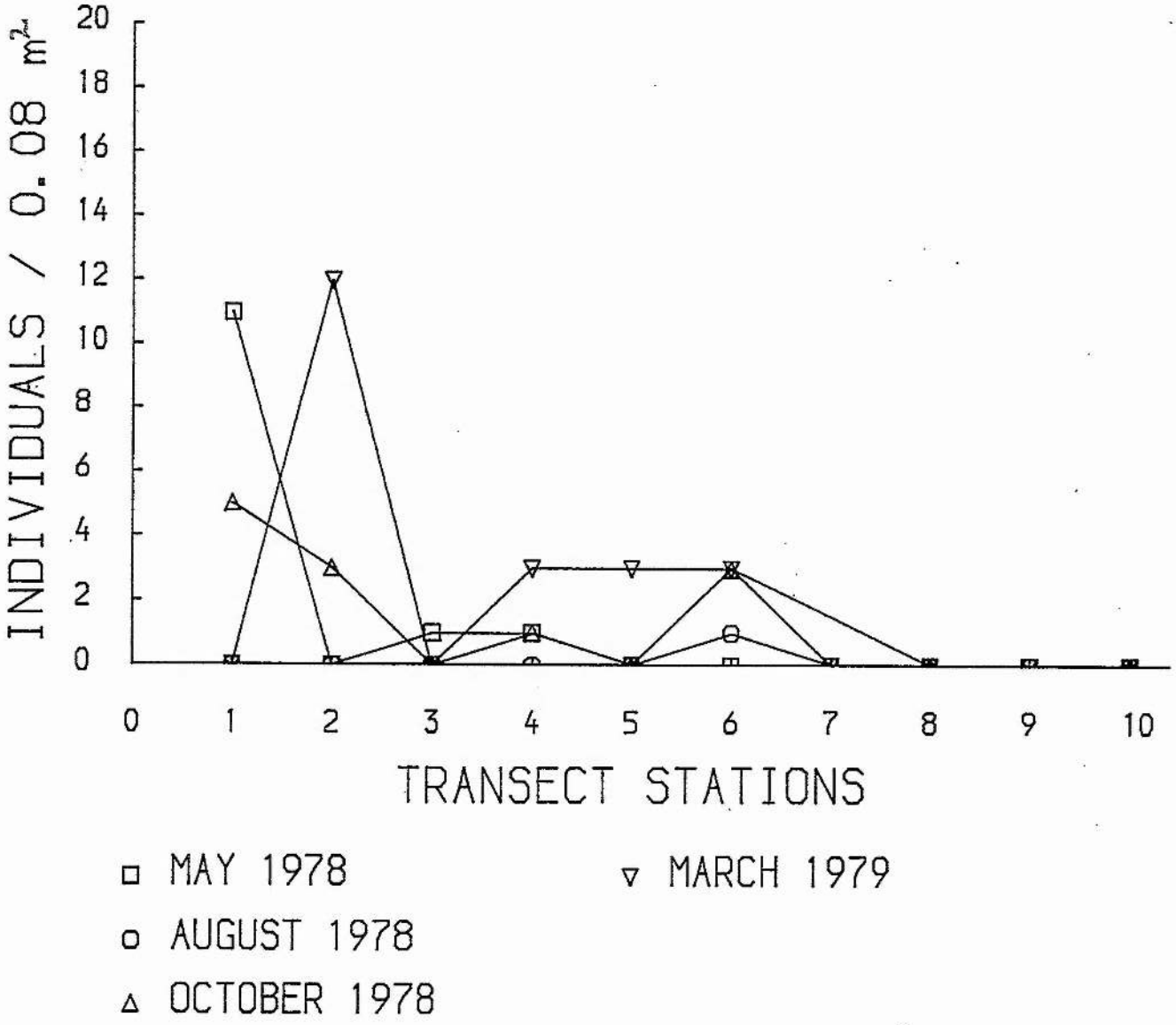
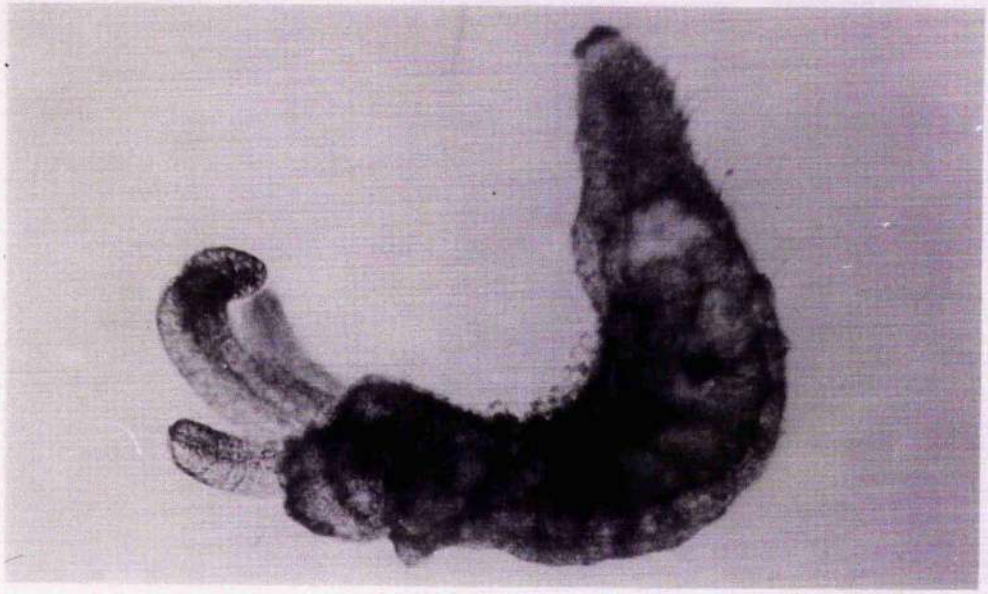


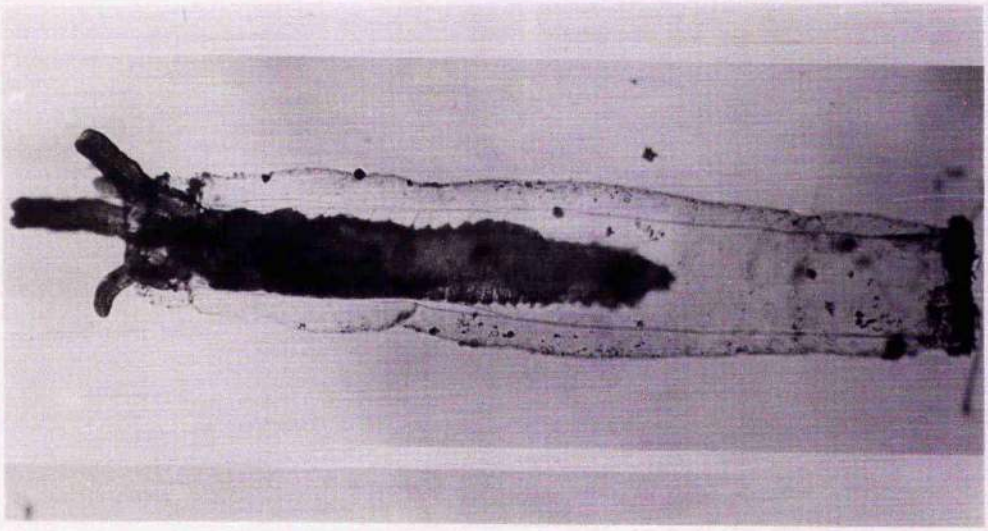
Figure 5-21

a. Aulophore larva of Lanice conchilega.
About 30 days old, removed from the tube.
Note three, short tentacles on left.
Scale: Larva is about 1 mm long

b. Aulophore larva of Lanice conchilega.
About 40 days old in larval tube.
Note short tentacles (five present) and oblique layers in the wall of the tube.
Scale: Tube is 0.6 mm wide.

c. Settled Lanice conchilega juvenile.
About 60 days old in larval tube.
Note light, extensile tentacles (lower left) and dark tube constructed of mucus and organic-mineral aggregates (upper right).
Scale: Tube is 1.0 mm wide.





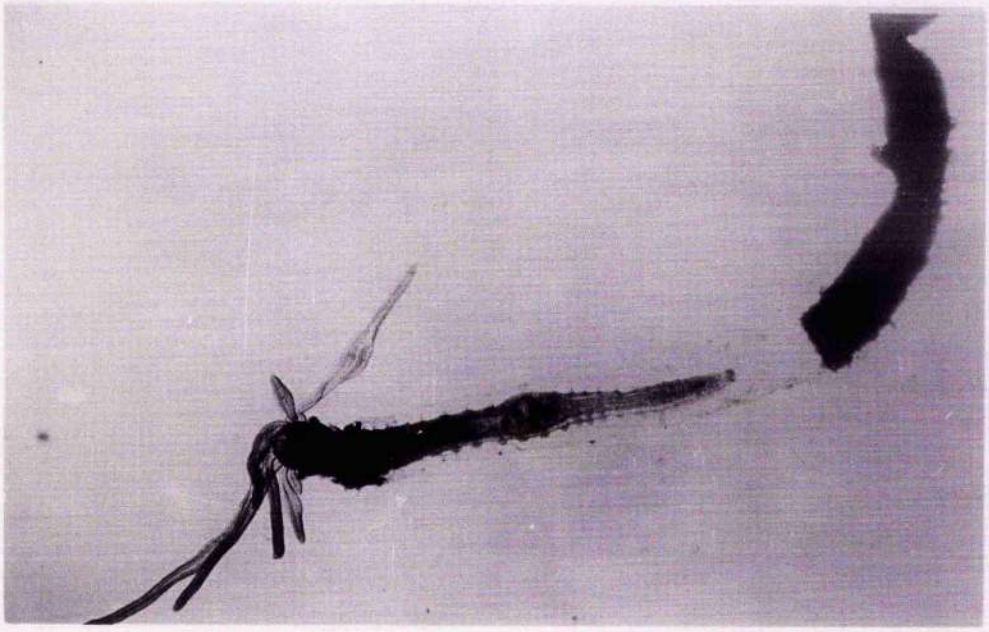
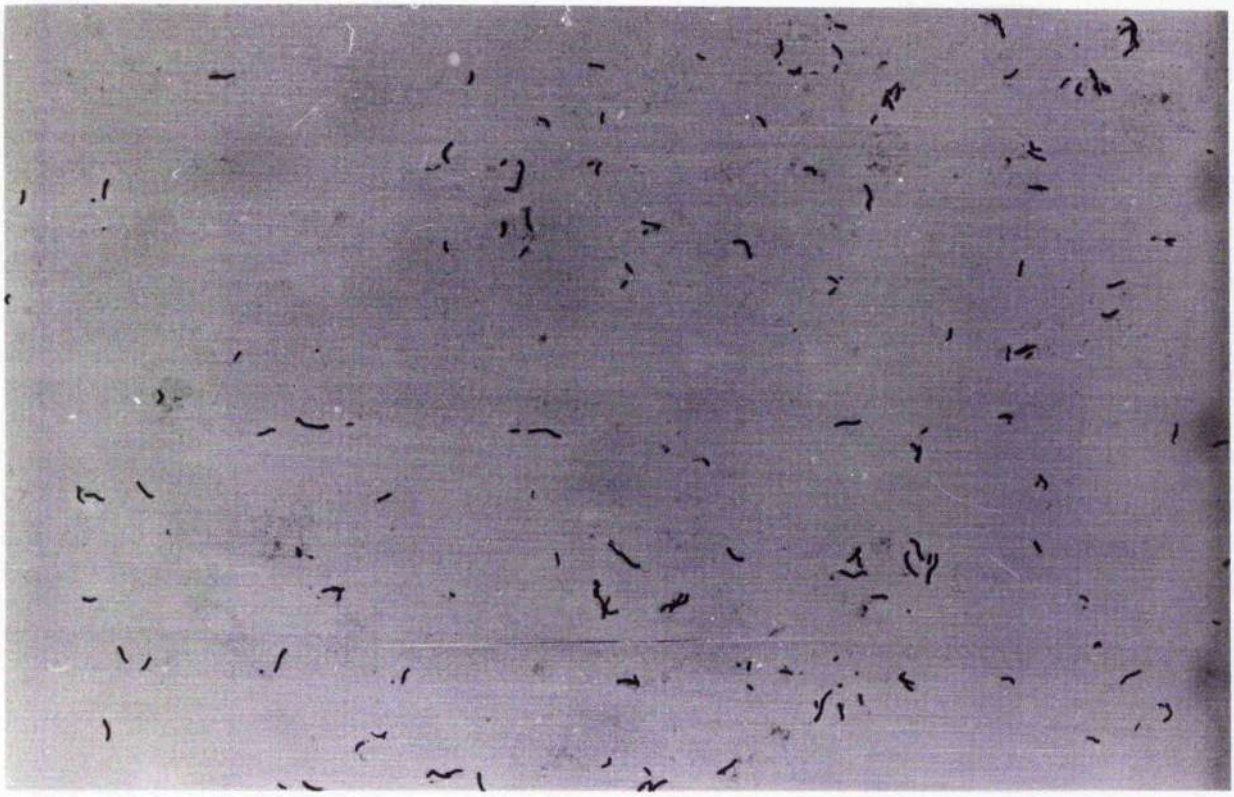


Figure 5-22

a. Juvenile Lanice conchilega settled in plastic film developing tray. Juveniles have constructed tubes from organic-mineral aggregates settled out of natural seawater. Tray has also been washed of all loose sediment and filled with filtered seawater.
Scale: x0.5

b. Juvenile Lanice conchilega settled in plastic film developing tray. Tray was emptied of seawater and filled with a suspension of sediment in filtered seawater. Organic-mineral aggregates and very fine sand have settled out of suspension and can be seen on the bottom of the tray. Dark thick lines are troughs in the base of the tray and the dark thin lines are the edges of the troughs. The pale patches are areas cleared of sediment by the feeding and tube-building activities of the worms 12 hours after addition of suspension. Same view as 5-22a.
Scale: x0.5



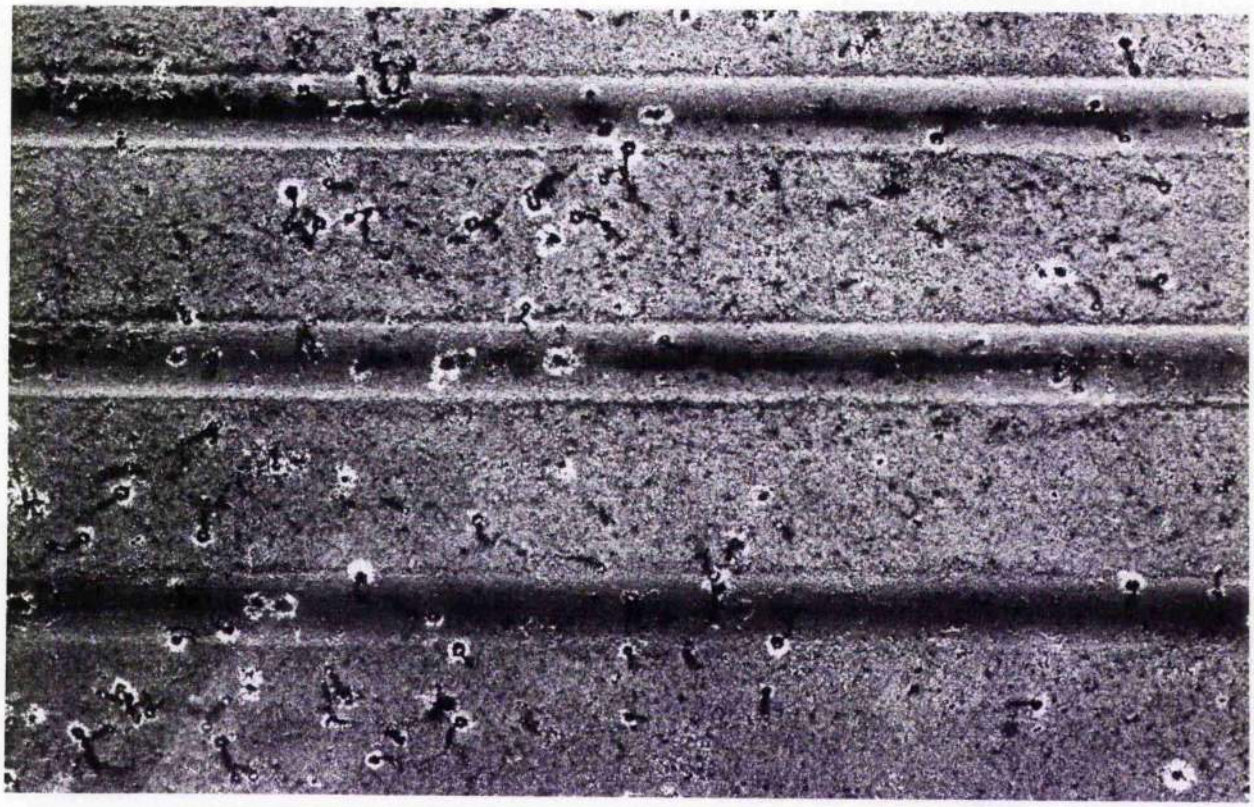
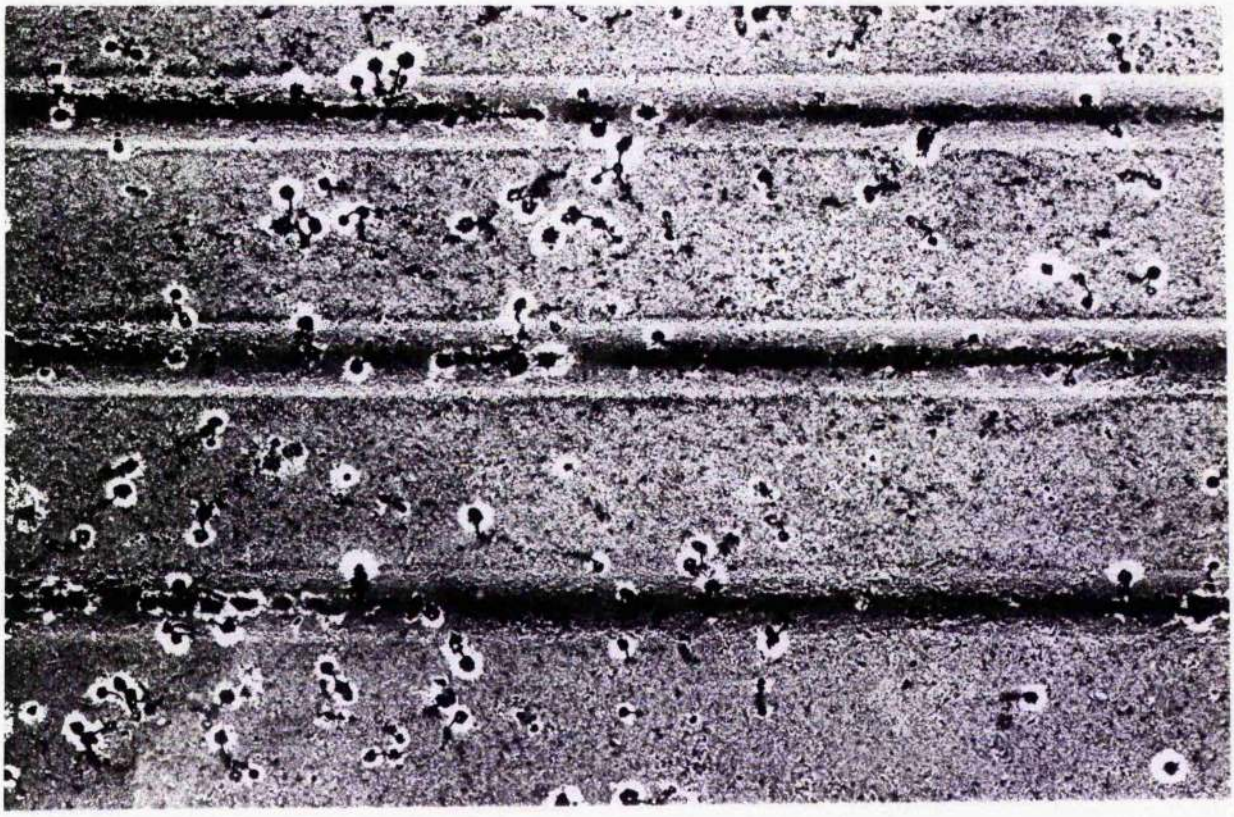


Figure 5-23

a. Juvenile Lanice conchilega settled in plastic developing tray. Juveniles have been deposit-feeding on organic-mineral aggregates allowed to settle out of suspension in seawater. Note white cleared patches and dark, circular rings of faeces. 18 hours after addition of new sediment. Same view as Figure 5-22 and below. Scale: x0.5

b. Same as above, 36 hours after addition of suspension. Note faecal rings (fr) not visible in 5-23a, these indicate extension of the tubes towards the top of the photograph. Note increase in size of cleared areas at both ends of single tubes (st), indicates deposit-feeding activity from both ends since 5-22a. Vertícle tube (vt) enlarged in Figure 24a.
Scale: x0.5



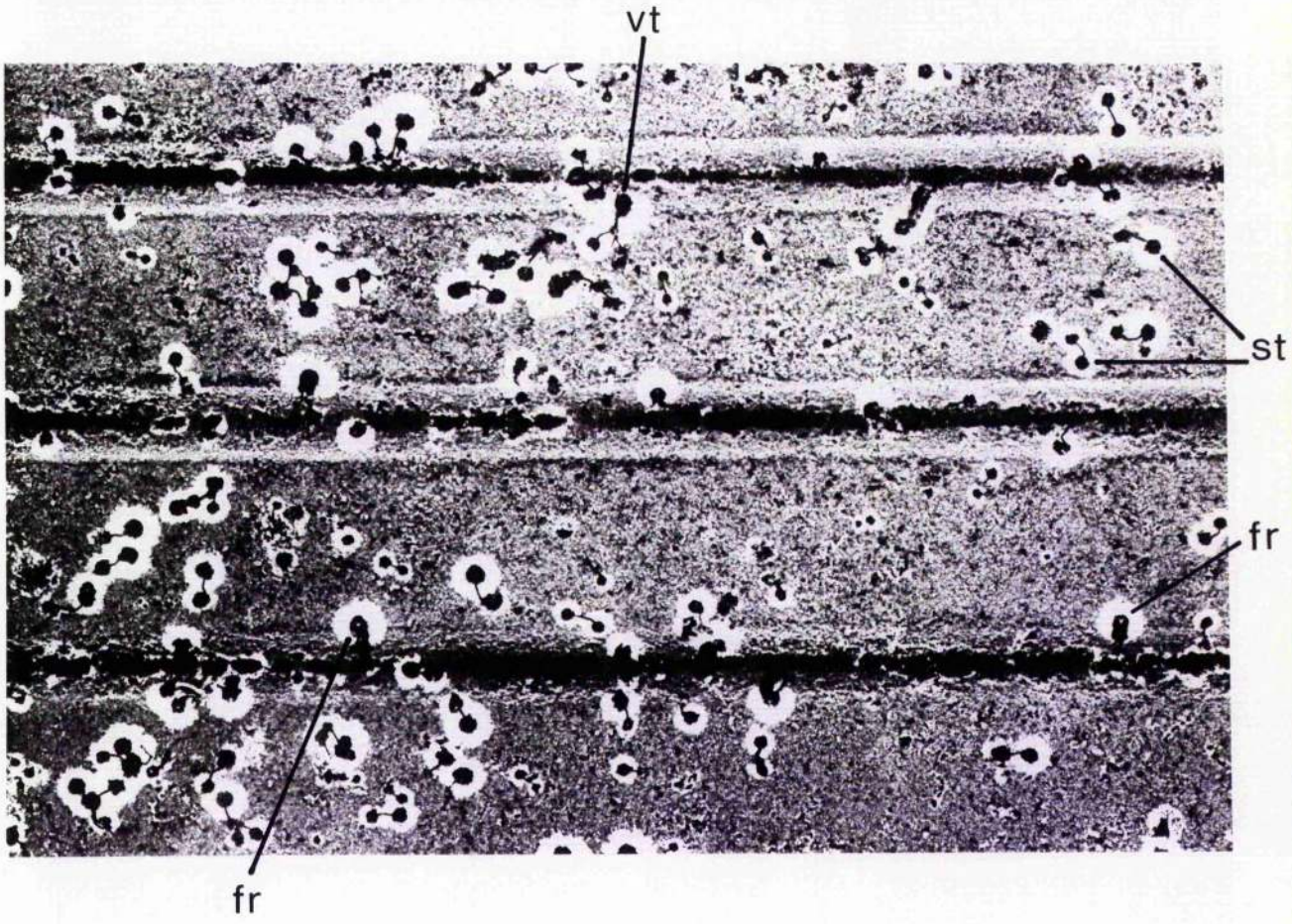

vt
st
fr
fr

Figure 5-24

a. Juvenile Lanice conchilega settled in plastic film developing tray. Worms have been deposit-feeding on organic-mineral aggregates allowed to settle out of continuously flowing seawater. 36 hours after rinsing of loose sediment. Worm on right has built a dark horizontal tube with four branches out of unsorted sediment (note clear larval tube attached to lower left branch). The worm on the right has cleared sediment from two circular areas around two of the branches and deposited faeces around these branches. The circles are presumed to be the limit of the tentacles' extension from the tube ends. This worm has also constructed a verticle tube from selected, coarse grains and added two fringe filaments to the tube end.
Scale: Horizontal tube is 1 mm wide.

b. Aggregation of tubes of settled juvenile Lanice conchilega at Tentsmuir Beach in July 1978. The small (2 mm diameter) tubes are clustered around larger, older tubes (some visible behind lens cap). Thalli of Enteromorpha sp. are dark stringy filaments in foreground and background. Foreground was disturbed by browsing of eider ducks.
Scale: Lens cap is 48 mm in diameter.

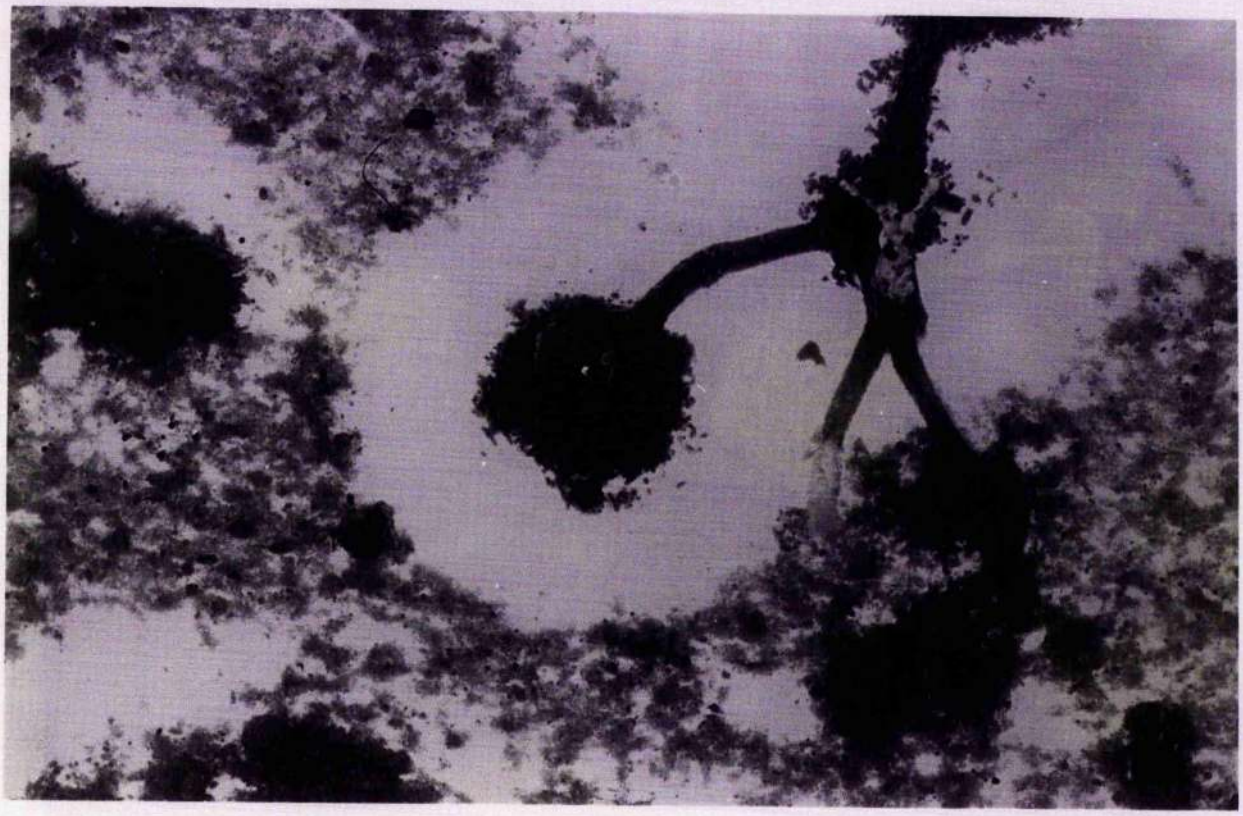
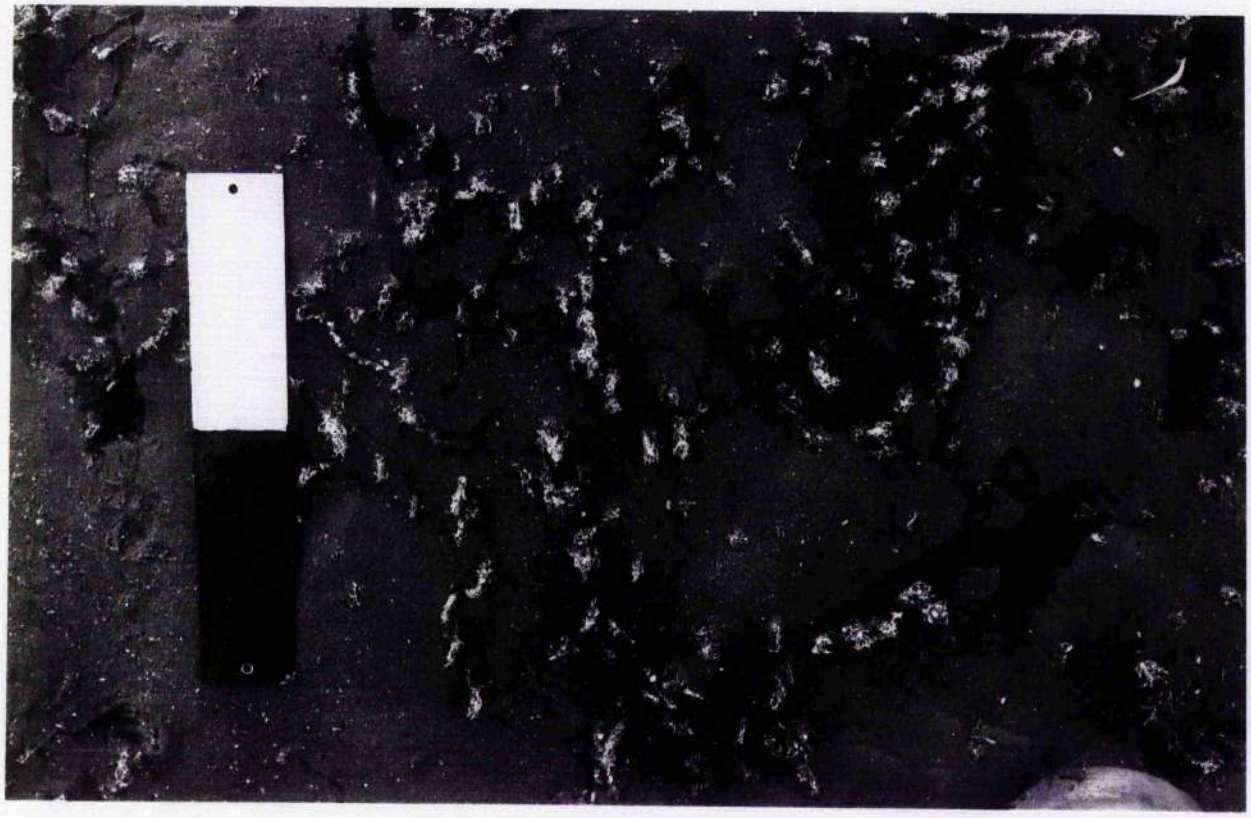
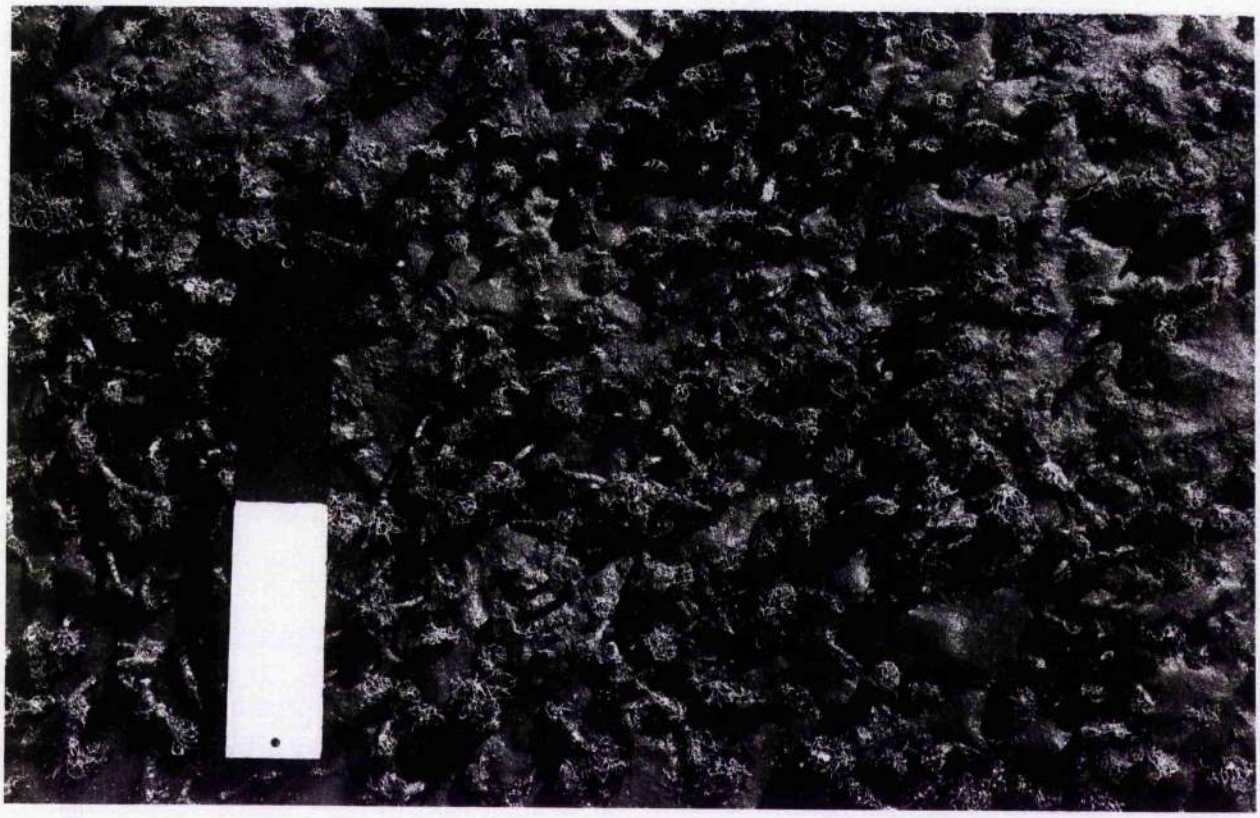


Figure 5-25

a. Lanice conchilega tubes from surface of algal-Lanice mound. Current flow was parallel to the bottom of the photograph, ebb flow to the right, flood to the left. Tube fringes were orientated perpendicular to the flow direction. Note arrangement of tubes in aggregated linear arrays perpendicular to flow direction.
Scale: bar is 20 cm long.

b. Apparent regular distribution of Lanice conchilega tubes from surface of Lanice flat. Current flow was parallel to bottom of the photograph, ebb to the right, flood to the left. Tube fringe orientation not clear in photograph. This apparent regular distibution may be a random filling of the available space with cylinders that cannot overlap (see Simberloff 1979).
Scale: bar is 20 cm long.





6 Chapter 6 Hydrodynamic analysis

6.1 Introduction

Many authors have commented on the elaborate tube top constructed by Lanice conchilega (Cuvier 1836, Dalyell 1851, Quatrefages 1865, Johnston 1865, Ehlers 1875, Cunningham and Ramage 1888, Watson 1890, 1916, McIntosh 1922, Hagmeier and Kändler 1927, Hagmeier 1951, Seilacher 1951, Ziegelmeier 1952, 1969). It has long been recognised as an aid in feeding and capture of particles (Watson 1890) but the precise mechanism has not previously been adequately described. In a recent review, Fauchald and Jumars (1979) discussed the literature on polychaete feeding and concluded that efforts to demonstrate facultative filter feeding by Lanice (Buhr 1976, Buhr and Winter 1977) failed to exclude the possibility, first raised by Seilacher (1951), that the worms feed primarily on resuspended bottom deposits. Jumars and Fauchald (1977) emphasized that the consideration of small scale geophysical processes is of primary importance in feeding studies of surface feeding benthic organisms.

Projecting tubes built by benthic organisms are a common feature of soft bottom environments (Ehlers 1875, Sanders 1956, Fager 1964, Woodin 1978, Brenchley 1979, Yingst and Rhoads 1978, Bailey-Brock 1979, Wilson 1979). Many marine organisms build cylindrical tubes that project vertically from the surface of mobile substrata but remain within the benthic bounday layer (e.g. Ampeliscid amphipods: Mills 1967, polychaete

worms: Fauchald and Jumars 1979). In benthic environments subjected to predictable fluid motion, the interaction of the fluid, tubes and substrate is a complex process that until recently has received little attention (see Taghon *et al.* 198 0, Eckman *et al.* 1981 and Jumars *et al.* 1981). The flow disturbance associated with projections in boundary layer flow is likely to have important effects on sediment movement and feeding behaviour in a variety of dynamic benthic environments. Fortunately, flow past cylinders, and more recently scour around projecting cylinders are topics widely investigated by hydrodynamicists. Indeed, Roper *et al.* (1967) were prepared to state: "that most aspects of the wake region behind an infinitely long circular cylinder in a uniform velocity field have been extensively investigated and documented" (see Morkovin 1964 for a review). This body of empirical and theoretical information is an invaluable aid in the study of physical influences on benthic tube dwellers.

6.2 Tube top of *Lanice conchilega*

6.2.1 Description of tube top

The tube of *Lanice conchilega* is constructed through mucoidal binding of shell fragments and mineral grains (Ziegelmeier 1952 1969). Below the sediment there is no selection of material, the burrow is lined with layers of muco-polysaccharides which bind the sediments of the burrow wall (Bielakoff *et al.* 1975). Above the sediment surface the tube is built of

selected grains and fragments of shell carefully attached with muco-polysaccharides (Wunderlich 1970). Generally, Lanice selects large grains and shell fragments to construct the projecting tube, and small grains and narrow fragments to build prolonged filaments that comprise a fan-shaped `fringe´. The precise nature of the tube top varies according to the material available, but the general form studied here consisted of two semicircular plates extended above the circular opening of the tube (4-5mm outside diameter). The plates and the cylindrical tube ended in irregular branching filaments (1-5 times as long as the diameter of the tube, Figure 6-1). The diameter of the filaments was dependent on the particle size available, but when a wide range of sizes was present the worm selected particles 0.5-1.0mm in the narrowest dimension and attached them lengthwise to build the fringe elements.

In the original description of Lanice conchilega (Pallas 1766, as Nereis conchilega) the author apparently did not observe the characteristic fringe on the tube top. His description contains an elaborate account of the tube, including the observation that the tube "emits a remarkable animal stench if it is burned", however he clearly obtained his specimens from tubes cast up on beaches by storms. For this reason his understanding of the life habits of Lanice and the structure of the tube was rather confused. Lanice tubes are frequently thrown up on beaches after storms, but examination of this material can be very misleading as the delicate fringe is usually abraded off by storm waves. Cuvier (1836) first correctly described the fringe: "et dont l´ouverture a ses bords prolongés en plusieurs petites branches formées des mêmes fragmens, et servent à loger les tentacules." (the aperture having its borders prolonged into several small branches formed of the same fragments, which serves to lodge

the tentacles). Although Cuvier's figure is very inaccurate it is clearly a drawing of Lanice conchilega (Cuvier 1836, plate 5, figure. 1). It is curious that despite the lengthy description of the habits of Lanice by Dalyell (1851) (as Terebella littoralis seu arenaria), subsequent authors confused the issue by asserting that the branching elements of the fringe were hollow (Quatrefages 1865, Cunningham and Ramage 1888; McIntosh 1922) and afforded some protection to the tentacles. Watson (1890) laid this dubious observation to rest but failed to describe accurately the tube building process in this or in a subsequent paper (1916). After 150 years of sporadic observation and description, no single author had a clear idea of: 1) the purpose of the fringe, or 2) the feeding behaviour of Lanice. It was not until Ziegelmeier (1952, 1969) conducted experiments in a simple flow tank that the unique adaptations of Lanice were revealed.

6.2.2 Use of the tube top

Seilacher (1951) correctly surmised from field evidence that the fringe is orientated perpendicular to the prevailing current, and he likened the fringe fan (Fransenfächer) to a type of fish trap (Reuse) placed across ebbing tidal channels. Ziegelmeier (1952) criticised this description and preferred a combination of a snare (Stellnetz) and a support for filter feeding tentacles as first suggested by Watson (1890). His primary objection to Seilacher's comparison was that a `Reuse' is apparently a conical shaped trap while the tube top of Lanice is a flat, fan shaped device. He failed, however, to fully appreciate the hydrodynamic effects of a projecting tube and the flaps and fringe.

Ziegelmeier (1969) suggested that the shape of the prostomial segments and their hydrodynamic damping effect might aid the worm in orientating the fan and adding material to the tube in a current. He also recognised that Lanice depends on turbulent resuspension in the benthic boundary layer for food but suggested that the fans function as baffles, slowing the water current and allowing sedimentation of fine particles between the tubes.

Ziegelmeier (1969) attempted to elicit a feeding response with free living plankton with no success and concluded that Lanice feeds on detritus. This contrasts with Buhr's (1976) experimental results of a 70.6-77.2% assimilation efficiency of suspended unicellular algae (Duneliella marina). Buhr used an apparatus and method pioneered by Winter (1973) which exposed the worms continuously to a high concentration of naked algal cells (40×10^6 cells litre $^{-1}$). The experimental chamber and food source represent a highly artificial environment and Buhr (1976) did not mention any observations of the feeding method employed by the worms under these circumstances. He concluded that Lanice can capture small particles from suspension in sufficient quantities to be described as a facultative suspension feeder. His study neglected the importance of resuspended detritus particles as a food source and the influence of the tube, fringe, substrate and currents on maintaining this resuspension. Buhr (1969) also suggested that only through filter feeding can Lanice maintain high population densities.

Buhr (1979) expanded on these conclusions and considered a wider scope of possible food particles but reiterated Ziegelmeier's suggestion that the primary effect of the fringe is to slow bottom currents and increase sedimentation. Buhr also favoured a sieve effect whereby large food

particles are caught in the fringe and collected by the tentacles. There is no direct evidence that the presence of the fringe increases sedimentation or slows bottom currents. There is also no observational evidence that Lanice feeds on particles large enough to be trapped by the fringe. The spacing between fringe elements was not observed to be less than 1mm, and although this does not prevent smaller particles from sticking to the fringe elements (if coated with mucus) it will be shown below that the fringe is a very inefficient filter.

6.2.3 Objective

The objective of this hydrodynamic investigation was to describe the influence of the projecting tubes of Lanice conchilega on the paths of suspended particles. The purpose of this description was to provide a background for elucidating the effects of the tubes on near-bottom sediment transport and the feeding behaviour of L. conchilega in unidirectional flow. In particular, I wished to investigate the conflicting suggestions regarding the effects of a projecting tube on the potential for capture of food particles. Seilacher (1951) suggested that the worms feed primarily on resuspended bottom deposits whereas Ziegelmeier (1952, 1969) and Buhr (1979) suggested that the baffle effect of the fringe should enhance sedimentation of food particles from turbid near-bottom water. The experiments were designed to measure trajectories of suspended particles and to test the multiple hypotheses that the presence of the tube with and without the fringe can cause: (1) increased numbers of particles with a trajectory towards the bed; (2) no significant change in particle

trajectories; (3) increased numbers of particles with a trajectory away from the bed. The experiments were conducted in a recirculating seawater flume. The objective of the design of the flume was to provide an experimental area where animals and natural sediment could be exposed to steady, unidirectional flow with repeatable turbulent flow conditions. The flow produced by this flume was not investigated in detail apart from simple dye observations and measurement of particle trajectories. Sediment transport studies concerned with evaluation of critical erosion velocities or theshold shear stress necessitate more complex flumes and measurement techniques.

6.3 Materials and Methods

6.3.1 Flume

A recirculating flume was constructed to produce steady, rough turbulent flow in controlled laboratory conditions. A vertical, free standing water channel was constructed of PVC pipe and reinforced glass fibre by Poly-Glass Ltd (Morecambe, Lancs, England) The flume construction is described in Appendix IV and illustrated in Appendix Figure II. Design principles of this type of flume are discussed in Vogel and LaBarbera (1978). For observational studies of aquatic animals vertical recirculating flumes have distinct advantages: the design and construction is relatively straightforward, the cost of materials is low, and vertical

flumes take minimal floor space.

Vertical velocity profiles are necessary to describe adequately the flow regime of a flume. It is possible, however, to derive a reasonable characterization of the flow by calculating the Reynolds number and boundary layer thickness.

The Reynolds number is a dimensionless value characterised by

$$Re = \frac{UL}{\nu}$$

where U is the mean-time-averaged flow velocity, L a characteristic length (in this case the boundary layer thickness) and ν the kinematic viscosity of the fluid. The boundary layer is a region of viscous flow with a thickness δ which develops next to any solid boundary due to forces of friction between the fluid and the boundary (Tritton 1977). The minimum thickness of this boundary layer can be approximated for flow along a flat floor if it is assumed that it has no thickness when the flow encounters the floor (for this flume, after it leaves the collimator).

In this idealized situation the flow in the boundary layer is initially laminar and after some distance becomes turbulent. It is difficult to predict where this transition occurs as there are many factors involved. The more important factors are: Reynolds number (where L is the downstream distance); presence and level of free stream turbulence; roughness of the floor; convection to or from the floor (Shames 1962). An increase in any or all of these factors will cause the transition to turbulent flow to occur further upstream.

In a recirculating flume with a rough floor, where any free stream turbulence generated is recirculated, it is very likely that the boundary layer is turbulent throughout the length of the flume. If this is so then the following equation defines the minimum boundary layer thickness

$$\delta = 0.38l\left(\frac{\nu}{Ul}\right)^{1/5}$$

Thus, for a downstream distance (l) of 80 cm and a mean cross-sectional flow velocity (U) of 10 cm s^{-1}

$$\delta = 3.8 \text{ cm}$$

And the minimum Reynolds number for flow in the test section is 3800. It is very likely that there is some thickness to the boundary layer when the flow leaves the collimator, so that δ = 3.8 cm and Re = 3800 must be considered minimum values.

The question remains whether this flow regime can be considered to approximate natural flow conditions. Once again, the natural flow regime can only be estimated as no velocity profiles are available. Due to fluctuations in velocity and bottom topography (large scale roughness) observed at Tentsmuir Beach it can be assumed that the flow there was unsteady and had a turbulent boundary layer at most states of the tide. The experimental flow conditions were selected to approximate mean time averaged flow over the sand flat collection area. Bed shear stress in the flume was sufficient to transport natural organic particulates in bedload but not to entrain the fine sand of the bed. Observations at the sand flat

at low tides and by diving supported this assumption. The sand flat was subject to sand transport in the small ripple regime during spring tide cycles (maximum mean velocities), while large suspended organic particles were seen at neap tides (minimum mean velocities).

6.3.2 Experimental conditions

Adult Lanice with well developed tube tops were collected from Tentsmuir Beach using rectangular can cores (20 x 20 cm, x 30 cm long) and the contents of the cores (tubes, worms and sediment) were immediately placed in sediment boxes. These boxes (glass fibre boxes, 20 x 20 x 30 cm with a 2cm lip drilled to accomodate brass bolts and a sealing ring) were maintained in a continuous seawater system at 12° C until needed. They were then mounted with the sediment surface level with the flume bottom and the tubes projecting into the test section of the flume.

Some boxes were placed in the flume after removing all the tube tops. Lanice will rebuild the tube top if provided with sediment and a natural fringe if fed and exposed to a gentle current (6-10 cm s^{-1} : Ziegelmeier 1969). Observations of particle behaviour were conducted with natural tube tops and with reconstructed tube tops before the fringes were constructed. This procedure allowed evaluation of the hydrodynamic effects of the fringe and tube separately.

6.3.3 Flow visualization

Milk was used as a non-toxic dye to observe flow conditions and patterns of flow disturbance (Crisp and Southward 1956). Milk was carefully injected into the upstream flow with a pipette (1 mm tip diameter). The pipette was held in an electrode manipulator and racked up and down to inject milk at different depths. Observations with the dye confirmed the presence of turbulent channel flow and a thin (<5 mm) sublayer close to the bed with the flow conditions detailed above. The sublayer, although not strictly laminar due to disturbance by the small-scale roughness (sand-size) of the bed, exhibited slower flow velocities and the milk was maintained in a distinct layer until it encountered larger roughness elements. In practice, the flume produced turbulent flow throughout the depth of the channel apart from thin layers at the free surface (contaminated with dust particles), rough floor, and smooth walls.

The qualities necessary to mimic organic particulates and fine sediment for visualization purposes were met with suspensions of denatured egg albumen. Denatured egg albumen has a density of 1.035 g cm^{-3} (Stecher 1968) at 20°C. Seawater has a density of 1.025 g cm^{-3} at 20°C (Hale 1965). Natural flocculent material has a density in seawater of 1.591 g cm^{-3} (McCave 1975). Denatured egg albumen is high in contrast, has low net density in seawater relative to natural particles (density of egg-density of seawater= 0.010 g cm^{-3}), has a discrete form, is non-diffusing, is insoluble in seawater and is inexpensive. Further

details of egg particle preparation and characteristics are given in Appendix V.

6.3.4 Photographic analysis

A photographic technique was developed to allow analysis of particle behaviour. A Pentax 35mm camera with a 100mm macrozoom lens (1:4) was mounted behind the tubes(s) under study. Two 150 w flood lamps with reflectors were mounted above the flume Previous techniques of photographing pathline of particles have relied on the use of high contrast models and high contrast particles. In order to produce photographs of natural tubes it was necessary to strike a balance between harsh lighting which gave excellent pathlines but overexposed tubes and diffuse lighting which gave good exposure of tubes but poorly defined pathlines. Floodlamps directed up at an angle of 30-40o to the vertical from in front of the flume gave the best results overall. A 275 w floodlamp directly over the tube produced the best conditions for high contrast photographs of pathlines.

A suspension of 30 g of fresh denatured egg particles in 1 l of seawater was added to the flume before each session of photography. Short exposures (1/8-1/2 s) were used for measurement of particle speed. Exposures of this duration produced an array of paths shorter than the film frame (Figure 6-4). This allowed accurate measurement of path length throughout the frame. Paths were measured in the part of the frame unaffected by the tube (upstream and above the tube) and the mean length of

10-15 paths was used as the free stream velocity for each photograph. Paths in the wake of the tube were measured, plotted on a diagram and recorded as a percentage of the measured free stream velocity. Paths were measured by projecting the film frame in a slide projector on an outline drawing of the tube and substratum. For each trial the camera position was unchanged, allowing the compilation of path positions and percentage velocities on a single diagram.

Photographs of egg particle paths (trajectories) were analysed for movement towards or away from the bed. Path angles were determined by measuring 5-10 tangents along the length of the path, taking the mean tangential angle as the instantaneous path angle. Observations of particle movement during experiments usually allowed definition of direction, any paths with indeterminate direction were not measured. Particles were not observed to descend vertically to the bed as any particles that struck the bed had a greater component of streamwise movement than vertical movement. Some particles leaving the bed near the tube were observed to have vertical path angles (little or no streamwise movement). This allowed discrimination of path direction near the bed in most cases. Flow within the wake (lee of the tube) was subject to upstream movement and shedding of complex vortices and was consequently more difficult to analyse. Measurements were made of long pathlines on long exposure photographs (1/2 sec) and only relate to pathlines near the bed. An upstream vector parallel to the bed was taken as 0^{o}, downstream 180^{o}, vertical away from the bed 90^{o} and vertical towards the bed 270^{o}. Net movement towards the bed (sedimentation) was defined as pathlines in contact with the bed with mean tangential angles of 180^{o}-270^{o} and net movement away from the bed (resuspension) as pathlines in contact with the bed with mean tangential

angles of 90°-180° (but see above).

6.4 Results

At all velocities observed (1-25 cm s^{-1}), flow past tubes produced a characteristic pattern of disturbance (Figure 6-1a).

1. Fluid near the top of the tube was accelerated over the tube and encountered some disturbance near the top of the wake.
2. Fluid that encountered the tube between the base and the top was accelerated around the tube and only rarely entrained in the wake.
3. Some of the fluid near the bed was accelerated around the base of the tube and entrained in an area of slow moving fluid in the lee of the tube (the wake). The entrained fluid rose in an erratic spiral to the top of the tube and was accelerated downstream by the disturbed flow near the top of the wake, or captured in eddies behind the tube which were periodically shed downstream.
4. Part of the fluid near the bed not entrained near the tube was entrained in the downstream portion of the wake, rose from the bed at a relatively shallow angle and was rapidly transported downstream. Particles and dyed fluid observed in the wake were found to result from entrainment of particles of the upstream bedload and fluid from the upstream near-bed sublayer. This indicates `resuspension´ of saltating or rolling grains and slow-moving fluid, rather than `capture´ of higher velocity suspended particles or fluid.

Observed patterns of flow disturbance in the tube wake increased movement of egg particles away from the bed (Table 6-2). Data were pooled for each set in Table 6-2, because no significant departure from homogeneity was found within the tube - present data (chi squared=1.1302 with eight degrees of freedom, $P>0.995$; expected values from marginal totals), or within the tubes-not-present data (chi squared=0.2659, with three degrees of freedom, $P>0.95$). Each set was tested against the null hypothesis of equal frequencies of movement away from and movement towards the bed. The results from experiments with tubes present showed a highly significant departure from the expected frequencies (chi squared=15.842 with one degree of freedom, $P<0.001$) the departure was an increase over the expected frequency for movement away from the bed.

Results from experiments with tubes not present showed a significant departure from the expected frequencies (chi squared=4.850 with one degree of freedom, $P<0.05$), in this case, however, the departure was an increase over the expected frequency for movement toward the bed.

Mean time-averaged particle velocities were determined by measuring relative lengths of pathlines to eliminate inconsistencies of experimental conditions. Pathline lengths were related to mean length of undisturbed pathlines calculated from 10-15 paths above the tubes for each photograph. Thus, particle velocities are expressed as percentages of an approximation of mean channel flow velocities. Velocities of particles within the wake were about 30% of the velocities of particles in undisturbed flow (Figure 6-2). This lower velocity was not significantly different between the wake of a single tube with no fringe and the wakes of two tubes with fringes

(P=0.1660, n=30 m=46, Wilcoxon rank sum test).

Pathlines of particles resuspended within the wake were observed to fall into two classes (Figure 6-3a and Table 6-3). Particles moving away from the bed within four tube diameters had low velocities and steep trajectory angles. Particles leaving the bed between four and ten tube diameters had higher velocities and shallow trajectory angles.

The observed trajectory angles for particles resuspended within four downstream tube diameters are significantly steeper than those resuspended further downstream ($P<<0.0003$, n=32 m=38, Wilcoxon rank sum test). Pathlines with the steepest trajectories (maximum 90^{o}) appeared to be concentrated within two downstream diameters, but a value for the distribution was not measured (but see Figure 6-2a,b).

At moderate flow velocities ($\bar{u}$=2-15 cm s^{-1}) worms were observed extending their tentacles into the wake, using the branched fringe as a support, and capturing resuspended egg particles and natural organic particulates (Figure 6-3b). Worms in tubes without fringes were also observed extending tentacles into the current but achieved less spread of the tentacles both vertically and horizontally and appeared to be less successful in particle capture.

6.5 Discussion

The characteristic flow disturbance patterns observed for tubes of Lanice conchilega in turbulent channel flow do not appear to be very sensitive to ambient flow velocities or fine details of tube geometry. Similar patterns have been observed for isolated projections in laminar boundary layer flow (Gregory and Walker 1951; Mochizuki 1961; Tani et al. 1962), and these patterns are not strongly dependent on flow regime, flow speed or obstacle shape (Sedney 1973).

The mechanics of a boundary layer (turbulent channel flow is effectively constrained flow with a turbulent boundary layer as thick as the channel depth) are often discussed in terms of momentum changes due to the action of pressure gradients (e.g. Moore and Masch 1963). In order to predict the consequences of flow perturbations downstream of an obstacle, however, arguments concerning vorticity are helpful (Lighthill 1963, Richardson 1968).

Vorticity describes rotation of the fluid, which involves changing orientations in space of fluid particles. A vortex line is a continuous line within the fluid of which the tangent at any point is the vector of vorticity at that point. A vortex filament is the fluid within a bundle of vortex lines which bound a tubular region of fluid (Tritton 1977).

In two-dimensional undisturbed flow along a flat bed, vortex filaments are generated transverse to the flow. These filaments are concentrated by the pressure field in front of any three-dimensional obstacle, causing three-dimensional separation and the formation of a horseshoe-shaped vortex system. In this system, the vortex filaments are wrapped around the obstacle and stretch downstream as a multi-ply vortex pair with axes parallel to the direction of the flow (Gregory and Walker 1951). This process of build-up and stretching of the vortex filaments leads to strong vortex motion at the front and sides of an obstacle (Richardson 1968).

Gregory and Walker (1951) and Mochizuki (1961) observed and photographed a pair of spiral smoke filaments rising vertically, close behind obstacles in boundary layers. When these filaments reached the top of the obstruction they trailed downstream in the centre of the wake. When the Reynolds number of the flow was increased (to an unspecified amount) the trailing filaments became unsteady and were shed as eddies. Morkovin (1972) reported that the near wake (close behind the obstacle) is fed by the near bed upstream flow and emptied by the spiral vortices. Tani et al. (1962) noted that the sense of rotation of the vortex filaments is such that momentum is transported towards the bed by the horseshoe vortex and away from the bed by the spiral filaments.

The particle trajectories observed within the wake of the individual tubes of Lanice can be related to these descriptions of vortex systems. The diagram in Figure 6-1b represents an idealised flow pattern past a three-dimensional tube in a laminar boundary layer. Particles carried near-bed flow or scoured from the bed by the horseshoe vortex (3 in Figure

6-1b) can be resuspended by the spiral vortex system (2 in Figure 6-1b) and carried downstream by the trailing filaments (1 in Figure 6-1b).

Although these detailed patterns of flow disturbance are described from laminar boundary layers, Morkovin (1972) stated that "Scattered evidence suggests that similar rising and sharp rearward bending of a mean flow-through takes place when the obstacle is immersed in a turbulent boundary layer." Apparently, enhanced local scour and resuspension of bedload are likely consequences of isolated small disturbances on erodable beds in the benthic boundary layer.

The `baffle effect´ of fan-shaped structures or fan-shaped arrays (Meyer 1973) has not previously been quantitatively examined. Buhr (1979) and Warner (1979) also suggested a baffle effect but go further in speculating that the reduction in near bottom current velocity produced by arrays of baffle elements will result in increased sedimentation. Meyer (1973) reported detailed dye observations of flow past unstalked crinoids in situ, and concluded that vertical, fan-shaped arrangements of arms aided particle capture by presenting maximum cross-sectional area to the flow. He also noted that the tube feet of Nemaster grandis were positioned on the lee side of a fan under conditions of persistent unidirectional flow and suggested that a region of velocity reduction and microturbulence on the down-current side made it easier for tube feet to capture particles in this orientation.

The effect of individual tubes of Lanice conchilega on flow clearly produces an area of reduced flow velocity (20% of the free stream velocity in the near wake, Figure 6-3a) but equally clearly does not result in direct sedimentation of suspended particulates (Table 6-2 and Figure 6-2). The flow disturbance created by the tubes could enhance particle capture efficiency through reduced flow speed and chaotic motion alone (Rubenstein and Koehl 1976). Perhaps more importantly, the flux of particulates from the sediment surface into the tube wake and the specific geometry of the flow patterns might enable the worms to place their tentacles in a position of maximum capture efficiency.

When the tentacles are extended along the top of the wake parallel to the ambient flow (Ziegelmeier 1969), they should experience minimum drag (Figure 6-3b). The movement of the resuspended particles with the lowest velocity, although chaotic, is generally up the lee of the tube perpendicular to ambient flow and then sharply rearward upon reaching the top of the wake (Figures 6-1 and 6-3b). These circumstances would produce maximum particle capture efficiency (Rubenstein and Koehl 1976) and have been observed to occur with natural organic particulates and egg particles in the flume.

The spatial limits of the wake envelope, and concomitantly the flow effects described above, are not known in detail. It would appear, however, that four tube diameters downstream represents a rough limit to the distribution of the spiral filaments which may result in strong resuspension of bedload and entrainment directly behind the tube. The spiral filaments and trailing filaments may, however, be shed periodically;

the effect of this (vortices travelling slowly downstream within the wake) can be seen in Figure 6-2a in the lower middle of the diagram, and 6-4 in the middle of each photograph.

Downstream of the spiral filaments the source of resuspension is likely to be scour from the horseshoe vortex filaments. The trajectories of particles outside the four diameters limit seem to preclude any advantage to the worm that has initiated the resuspension. This limit may represent an optimum spacing for aggregated populations of Lanice, but care must be taken in this interpretation as the effect of tube height was not fully investigated and this `limit' may be related to many geometric factors other than tube diameter.

Buhr and Winter (1977) and Buhr (1979) reported dense subtidal aggregations of Lanice which may exceed this spacing limit even for an overdispersed (regularly spaced) population. They did not measure spatial dispersion, but preliminary observations at Tentsmuir indicated that Lanice aggregated in linear arrays perpendicular to the dominant current direction, allowing greater space between tubes in the streamwise directions and less space in the cross stream directions (Figure 5-25a).

These speculations on optimal spacing ignore any harmonic effects between tube wakes which can have a profound influence on the flow disturbance (Zdravkovich 1977), particularly when vortex shedding occurs (Tritton 1977). Arrays of tubes (or roughness elements) may produce effects which at present are unpredictable but they are likely to increase bed movement up to a critical density (one-twelfth of the plan area of the bottom occupied by tubes or elements) and decrease bed movement above that

density (Nowell and Church 1979). Eckman et al. (1981) provided a plot of this critical density expressed as a relationship between tube size and density. Reported maximum densities and estimated tube diameters for Lanice tubes (20,000 m^{-2} x 2 mm, 10,000 m^{-2} x 4mm, Buhr and Winter 1977; 4,000 m^{-2} x 5mm pers obs. 1978) fall on or slightly above this critical level. Experiments reported by Eckman et al. (1981) failed to produce bed stabilization widely assumed to result from dense arrays of tubes. Rhoads et al. (1978), however, reported observations that supported the suggestion that arrays of tubes may have a stabilizing effect on fine sediments by increasing the thickness of the viscous sublayer.

It is important to emphasize that roughness elements that produce flow disturbances have two primary effects on boundary layer flow: they create localized areas of increased and decreased flow velocity with a net loss of flow energy through friction, and they produce flow perturbations (shed vortices, trailing filaments, turbulent wakes) that extend downstream. It seems logical that arrays of roughness elements should also produce a net loss of flow energy and result in net sedimentation as predicted by Buhr (1979) and Warner (1979). This `baffle effect' sedimentation has not been demonstrated and the poorly understood effects of flow disturbance within arrays may affect the result. It is not possible at present to predict the effects of tube arrays on net resuspension and net deposition, but clearly the density and dispersion of individual roughness elements must be carefully considered in any investigations of this problem.

The methods and results reported in this study may not be suitable for addressing the problem of the effects of arrays of projecting tubes. The visualization techniques were not successful with large numbers of tubes or in plan-orientated observations due to lack of contrast. Although the conclusions are at present limited to isolated projections within the boundary layer on non-cohesive substrata, it seems clear that small-scale flow disturbance resuspended organic particulates. There is no direct evidence in these results that indicates increased sedimentation as a result of isolated flow disturbance.

Table 6-1

Estimated hydrodynamic characteristics of denatured (hard-boiled) egg albumen particles used for flow visualization. Derivation of characteristics based on denatured albumen density of 1035 Kg m^{-3} (ρegg) and seawater density of 1025 Kg m^{-3} (ρw). Shields threshold criterion (θ_t) obtained from Yalin curve (Miller et al. 1977, Figure 4) knowing $\left[\frac{\rho_{egg} - \rho_w g d^3}{\rho_w \nu^2}\right]^{1/2} = \sqrt{H}$ (Yalin parameter).

$$\theta_t = \frac{\tau_{o\,crit}}{(\rho_s - \rho_w) g d}$$

where ρ_s = density of particles
ρ_w = density of fluid
g = grav. constant
d = equivalent sphere diameters
ν = dynamic viscosity
$\tau_{o\,crit}$ = critical threshold stress

Knowing the value of the Yalin parameter, diameters of particles with higher densities were obtained by solving for d

$$\left[\frac{H(\rho_w \nu^2)}{g(\rho_s - \rho_w)}\right]^{1/3} = d$$

$\rho_{oma} = 1068\ kg\ m^{-3}$

$\rho_{qtz} = 2650\ kg\ m^{-3}$

In this way the egg particles can be compared with large organic-mineral aggregates (oma) and quartz (qtz). Density of organic-mineral aggregates was estimated by McCave (1975), the value used is that given for particles 0.181 mm in diameter.

Table 6-1 (con't).

Theoretical terminal settling velocities of egg particles were determined from Yalin's equation

$$W = 0.056 \frac{\rho_{egg} - \rho_w g d^2}{\nu \rho_w}$$

This equation is valid for particles with grain Reynolds number $(\frac{WD}{V}) < \approx 1$ and Yalin parameter $(H) < \approx 18$. For larger grains (in this case 1.000 mm) the value of W was obtained from a curve (Yalin 1972, Figure 3.2). The diameters of organic-mineral aggregates with equivalent settling velocities were interpolated from the estimated settling velocities of McCave (1975). The diameters of quartz particles with equivalent settling velocities were obtained by solving the equation for d

$$d = \left[\frac{\left(\frac{W}{0.056}\right) \nu \rho_w}{(\rho_s - \rho_w) g} \right]^{1/2}$$

and for the largest particle size by plotting W versus d using values obtained from Yalin (1972, Figure 3.2).

Table 6-1a Diameters with equivalent Shields threshold criterion.

Diameter of egg particles (mm)	0.25	0.50	1.00
Diameter of oma particles (mm)	0.15	0.31	0.61
Diameter of qtz particles (mm)	0.046	0.092	0.183
Shields threshold criterion Θ_t	0.150	0.068	0.052

Table Diameters with equivalent theoretical settling velocity.

Diameter of egg particles (mm)	0.25	0.50	1.00
Diameter of oma particles (mm)	0.135	0.320	0.750
Diameter of qtz particles (mm)	0.020	0.039	0.070
Theoretical settling velocity (10^{-3} cm s^{-1})	32	128	325

Table 3-2

Increase in resuspension of egg particles within wake envelope of Lanice conchilega tubes. Total of results from six photographs (1/2s) taken at 30 sec intervals in recirculating flume with a mean channel flow velocity of 10 cm s^{-1}. Wake envelope is directly downstream of tube, height = tube, width = twice tube diameter and downstream length = five tube diameters. Count with no tubes present made on equivalent areas (tube diameter 0.5 cm).

Experimental conditions	Egg particle grain size μm	Particle pathlines with net movement towards bed	Particle pathlines with net movement away from bed
1 tube, no fringe	250- 500	8	17
1 tube, no fringe	250- 500	5	10
1 tube, no fringe	500-1000	11	17
1 tube, fringe	250- 500	10	21
1 tube, fringe	500-1000	9	17
2 tubes, fringes	250- 500	7	10
2 tubes, fringes	250- 500	6	11
2 tubes, fringes	500-1000	12	17
2 tubes, fringes	500-1000	10	17
	(Total)	(78)	(137)
No tubes present	250- 500	13	12
No tubes present	250- 500	17	15
No tubes present	500-1000	8	9
No tubes present	500-1000	10	6
	(Total)	(48)	(42)

Table 6-3

Mean velocities of egg particle pathlines relative to undisturbed channel flow velocities and mean trajectory angles of pathlines relative to downstream flow direction. Velocities were obtained from pathlines and vectors in Fig. 6-3a and are expressed as a percentage of channel flow velocity (100%). Trajectory angles were obtained from twenty-six photographs and are expressed in degrees where 180° is downstream and 0° is upstream. The results were grouped in two classes related to distance downstream of a tube.

6-3a

	Point of departure from the bed (in tube diameters downstream)	
	4	4, 10
Velocity	22.6 ± 2.6% n=53	60.5 ± 1.2% [a] n=11
Trajectory	100.3 ± 5.6% n=38	149.7 ± 4.1% n=32

a. confidence limits from log transformation

Figure 6-1

Flow disturbance around a tube of Lanice conchilega. The tube end is extended into two semi-circular plates arranged normal to the flow direction. The plates and the cylindrical tube end in irregular branched fringe filaments which are 1-5 times as long as the diameter of the tube. The tubes are 0.5 cm in diameter.

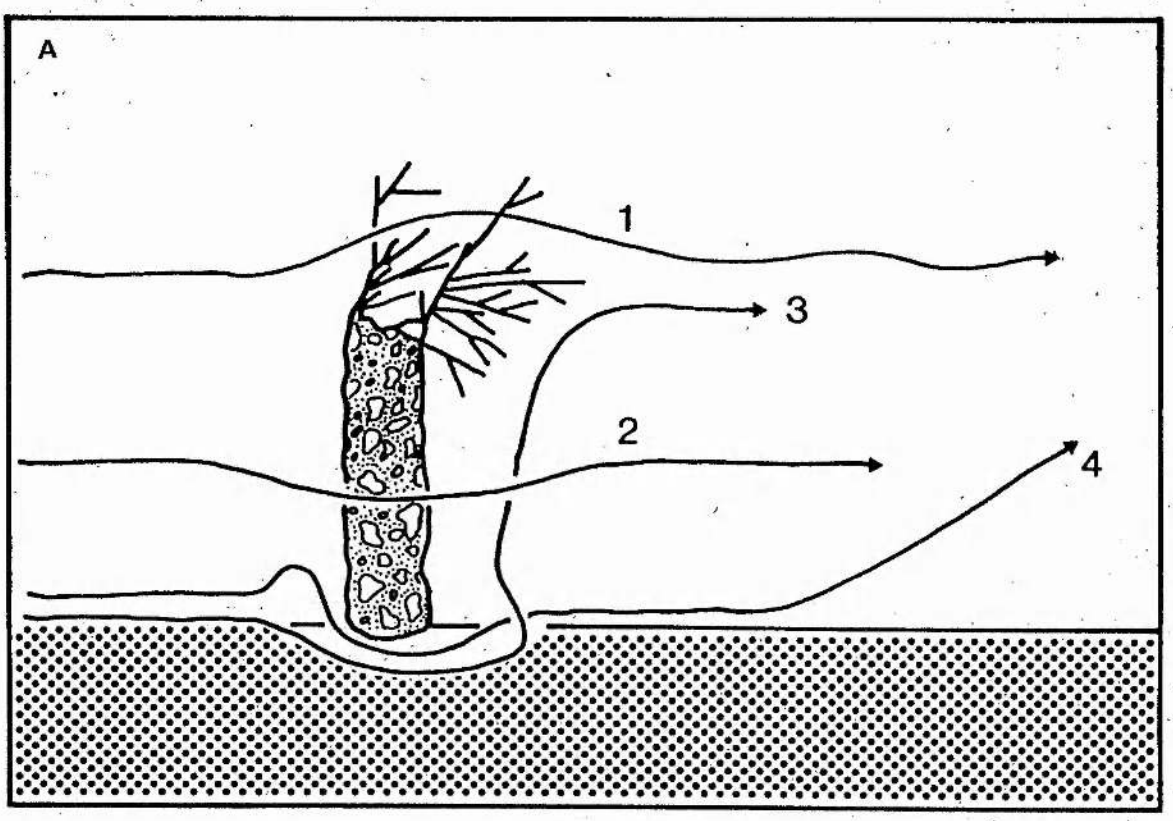
a. Flow was from left to right. Arrows represent generalised flow patterns observed in flume experiments. Numbers refer to description in text (Section 6.4).

b. Idealised effect of projecting tube of Lanice in undisturbed laminar boundary-layer flow. Lines represent vortex filaments and small arrows indicate sense of rotation, broad arrow represents dominant flow direction. Derived from flume observations and results presented by Gregory and Walker 1951; Thwaites 1960; Mochizuki 1961 and Tani et al. 1962).

1. Trailing vortex filaments

2. Spiral vortex filaments

3. Horseshoe vortex filaments (see Section 6.5).


A
1
3
2
4

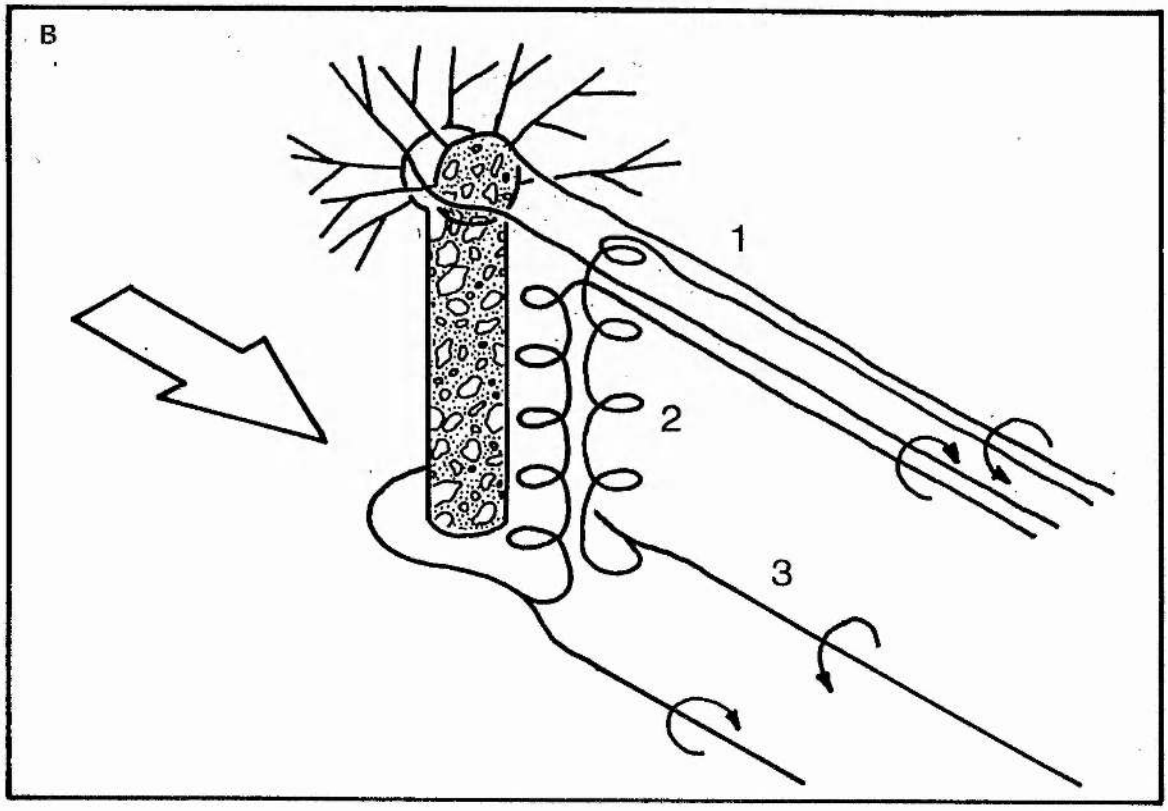

B
1
2
3

Figure 6-2

Velocities of egg particles resuspended in the wake envelopes of Lanice conchilega tubes, measured from pathlines on flume photographs. Vector length represents length of pathlines relative to mean length of undisturbed pathlines calculated for each photograph. Lengths of pathlines are equivalent to time averaged velocities of particles. Reference vector (100% of channel flow velocity) in upper left.

Dot lines are observed pathlines. Channel flow velocity 10-11 cm s^{-1} in all photographs.

a. Adult tube, built in flume, fringe not present. Summary of eight photographs (1/8 - 1/2 second exposure). Mean percentage of channel flow velocity of particles within wake envelope is 35.08 ± 6.27 (at 95% confidence level, n=46).

b. Adult tubes, natural spacing, orientation and fringes. Summary of six photographs (1/8 - 1/2 second). Mean percentage of channel flow velocity of particles within wake envelopes is 31.47 ± 7.64 (95% c.l., n=30).

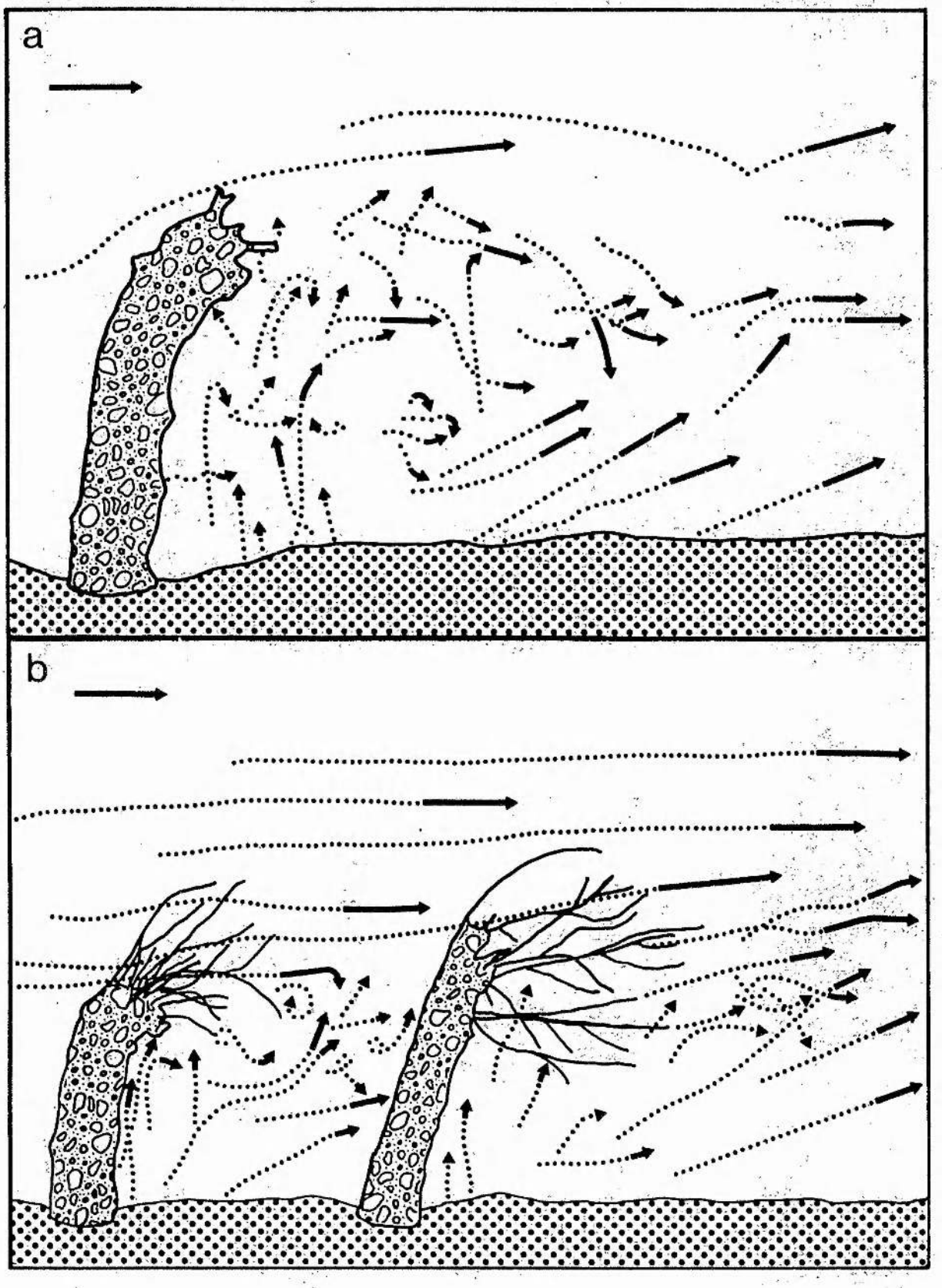
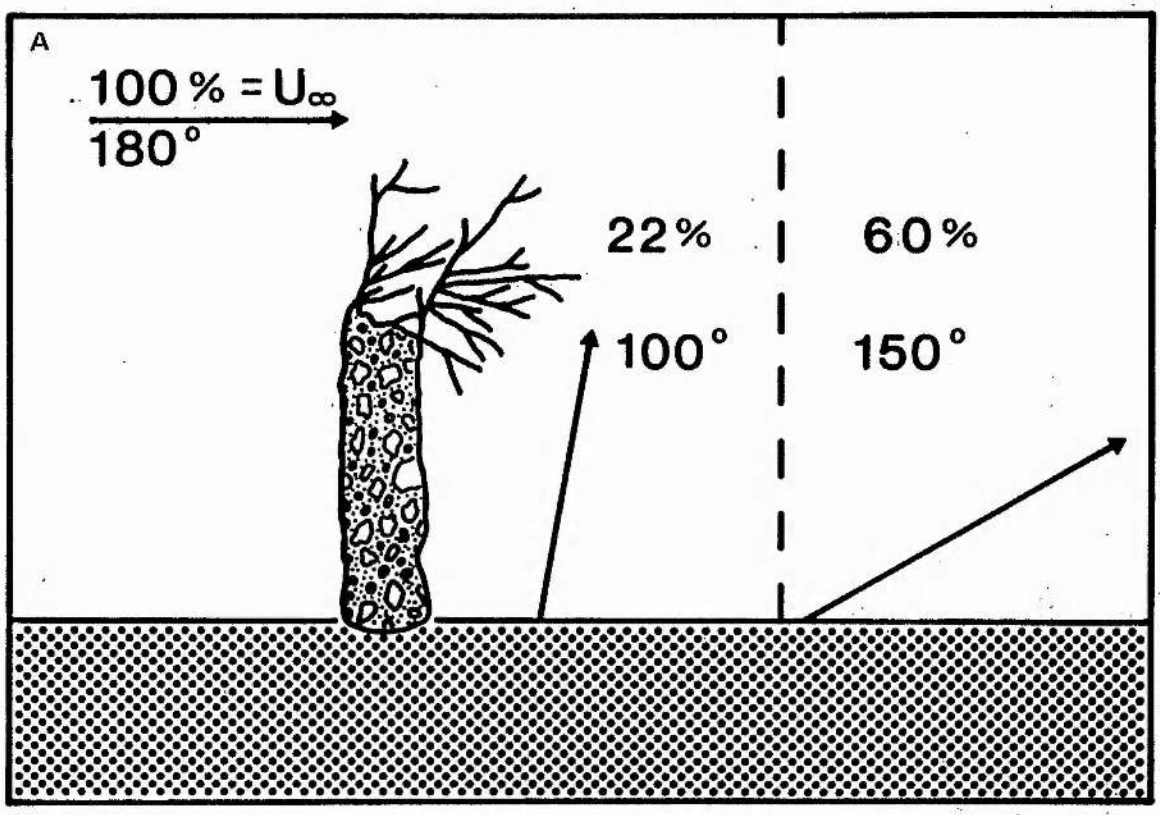

a
b

Figure 6-3

a. Mean angles and relative velocities of pathlines downstream of tube of Lanice conchilega. Summary of results from twenty-six photographs (angles) and Figure 2 (velocities). Length of arrows is not significant. Downstream is defined as 180°, and undisturbed channel flow as U (100%). Flow is from left to right.

b. Lanice conchilega capturing egg particles resuspended downstream of tube. Flow is from left to right. The tube is depicted with the foreground removed to show the position of the worm. The small arborescent structures projecting from the top of the worm are branchiae (gills). The highly extensible mucus-coated tentacles (open filaments) are shown resting on the fringe filaments (stippled filaments) and extending downstream, with the flow. In this position the tentacles will encounter slow moving particles advected from the bed by the resuspension mechanism illustrated in Figure 6-1a and b.


A
100 % = U∞
180°
22%
60%
100°
150°

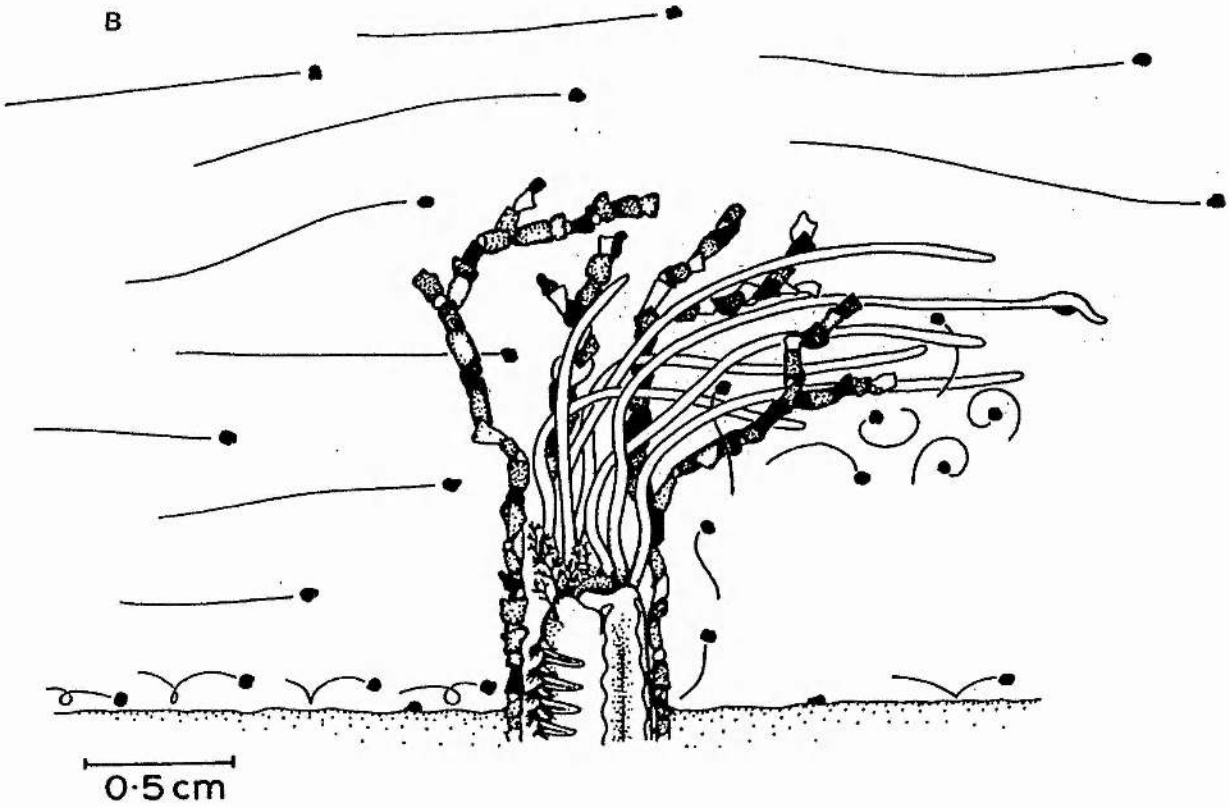

B
0·5 cm

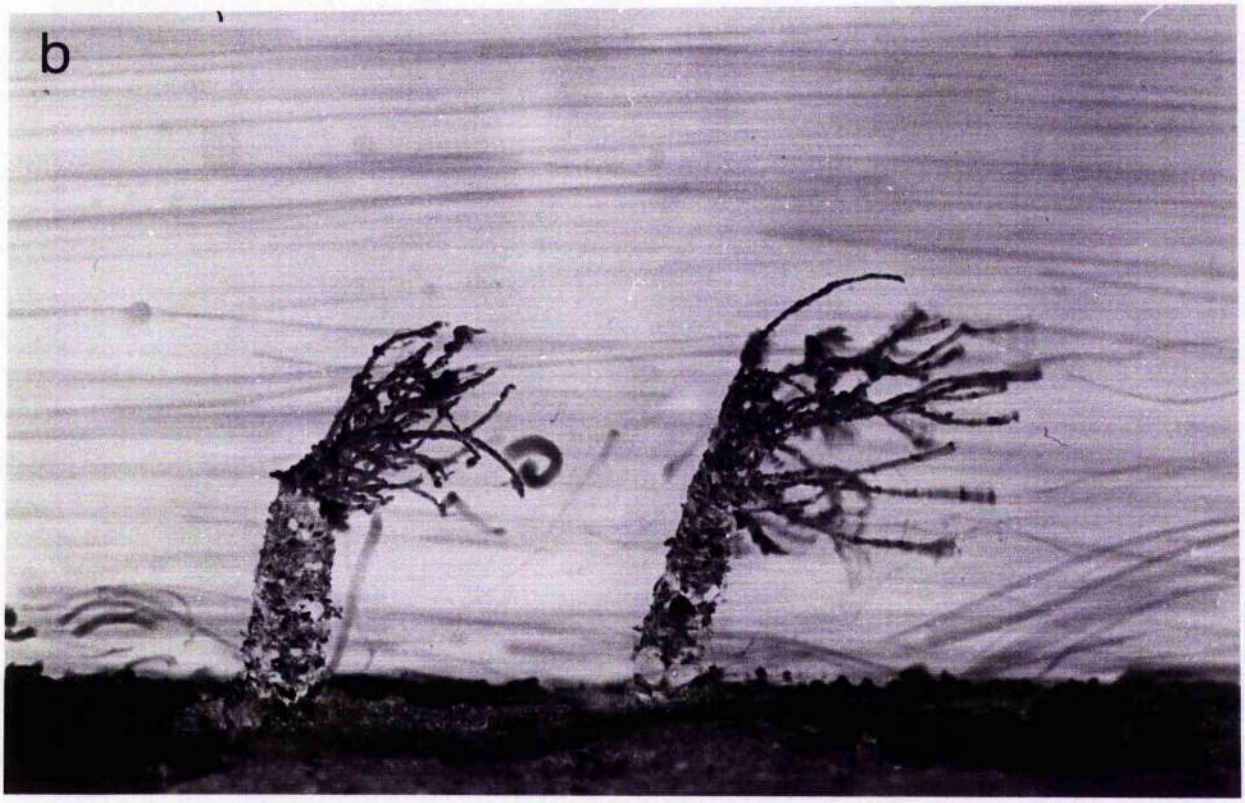
Figure 6-4

Photographs of egg particle paths around tubes of Lanice conchilega in seawater flume. Flow was from left to right.

a. Adult tube of Lanice conchilega, built in flume, fringe not present. Channel flow velocity 10cm s^{-1}, water depth 10cm. Photograph taken with a Pentax with 100mm macrozoom lens and a 1/8 second exposure.

b. Adult tubes of Lanice conchilega, natural spacing, orientation and fringes. Channel flow velocity 11cm s^{-1}, water depth 10cm. Photograph details are as above but with 1/2 second exposure. Tubes are approximately 0.5cm in diameter in both photographs. Compare with Figure 6-2.


a


b

APPENDIX I

Sediment sample collection and treatment

Twenty sediment samples were collected from the study area at Tentsmuir Beach (see Appendix Figure I for location of samples). Ten samples were collected on 18 August 1978, one from each station on the established transect. Ten samples were collected on 16 April 1980: eight from stations 1-8, one from an algal-Lanice mound north of station 5 (S_1) and one from a small ripple field south of station 2 (S_2).

Samples were collected from transect stations with a plastic core tube 7 cm long and 2 cm in diameter (22 cm^3). Each sample was collected 1 m north of station markers to avoid effects of ebb current disturbance around markers. Samples S_1 and S_2 were collected by scraping the top 1 cm of sediment from an area of 25 cm^2.

All samples were oven-dried at 40° C and coned and quartered to produce two sub-samples, each roughly 25 g. Sub-samples from August 1978 stations were treated separately: both groups of sub-samples were dried, weighed, washed four times in distilled water, dried and weighed; one group was then treated with 10% hydrochloric acid to remove calcium carbonate ($CaCO_3$), washed four times in distilled water, dried and weighed; loss of weight after treatment was recorded as $CaCO_3$ (Carver 1971). Samples from April 1980 were not treated separately: sub-samples were dried, weighed, washed four times in distilled water, dried and weighed.

All subsamples were placed in a nest of six sieves (-1.0 - 4.0 phi at 1 phi intervals), sieved for 10 minutes on a sieve shaker and each fraction weighed to the nearest 0.01 g. No further analysis was done on the fraction passing through the finest mesh (0.063 mm, 4 phi) as in all cases this accounted for less that 0.1% of the sample weight.

The Folk and Ward measures of mean, sorting, skewness and kurtosis were calculated using a computer program for granulometric analysis (Allen 1970) modified by Eastwood.

APPENDIX II

Infaunal sample collection and treatment

Fifty-one infaunal samples were collected from the study area at Tentsmuir Beach in 1978 and 1979 (see Appendix Table I and Appendix Figure I). Five samples were collected in April 1978 as part of a preliminary survey (AM, MS, MK, LX, PF). Ten samples were collected in May and August 1978, one from each station on the established transect (1p-10p, 1j-10j). Two samples were collected in July 1978 adjacent to the washed core described in Chapter 4 (HD1, HD2). Eight samples were collected in October 1978 from the transect stations (1i-6i, 8i, 10i); stations 7 and 9 were submerged and no samples were collected from them at this time. Twelve samples were collected in March 1979, one from each transect station (1f-10f); one within (EBT1), and one adjacent to (EBT2) an eider browsing trace. Two samples were collected in April 1979 as a pre-treatment control for the transplantation of Lanice (LTC1, LTC2). Two samples were collected in October 1979 at the end of the Lanice transplant experiment: one within the transplant area (LTT1) and one adjacent to it (LTC3).

All samples were collected with a simple can-core: a 1 litre oil can with the bottom removed. Howard and Reineck (1972) considered this the simplest and most inexpensive coring tool available. The litre oil can took a sample 30 cm deep with a surface area of 200 cm^2. Each sample consisted of the pooled cores of 4 can-cores taken from random coordinates near the station poles. The pooled sample represents 0.08 m^2 surface area sampled to a depth of 30 cm (24,000 cm^3).

Appendix II

Lanice tubes can extend up to 50 cm vertically into the substratum (Wohlenberg 1937) and although U-tubes were recovered with this can-core technique (indication of complete tube), the cores probably undersampled the deep burrowing fauna (Ensis siliqua) and those species that could escape down deep Lanice tubes (Lanice conchilega, Eumida sanguinea, Harmothoë lunulata, Anaitides maculata, Nereis pelagica, Amphiporous lactifloreus, Scoloplos armiger).

All cores were washed at the beach through a nylon sieve with a 0.5 mm mesh. The fauna retained on the sieve was carefully washed into a bucket and removed to the lab for preservation and analysis. Most samples were sorted immediately, identified to species and frozen for later analysis of wet weight and dry weight. All of the frozen samples were lost during a power cut, but 12 samples had already been analysed as described below. This technique of preserving benthic samples by freezing, results in more accurate wet and dry weights (Holme and McIntyre 1971) but prevents re-examination of material to check identification. Thus, in some samples differentiating polychaete species has proved difficult (see notes in Appendix III). Species abundances, sampling dates, and environmental division classification for all fifty-one samples are presented in Appendix Table I. A full annotated species list is presented in Appendix III.

Appendix II

Samples analysed for biomass (ash-free dry weight) were treated as follows. Large species were weighed individually and smaller species were grouped by phyla or, if abundant, by species. Shells, tubes and sand were removed manually from the soft tissues which were lightly dried with paper towels and weighed in pre-weighed crucibles. The samples were then dried for 3 days at 60° C in a ventilated oven, weighed, placed in a muffle furnace at 600° C for 2 hours, and weighed again. The weight loss at 600° C represents the ash-free dry weight and is used as a measure of biomass (Holmes and McIntyre 1971 Beukema 1976). The biomass values for HD1 and HD2 are presented in Appendix Table II and the values for samples 1p-10p are presented in Appendix Table III.

APPENDIX III

SPECIES LIST

Nemertinea
- Enopla
  - Hoplonemertini
    - Amphiporidae
      - *Amphiporus lactifloreus* (Johnston)

Annelida
- Polychaeta
  - Orbiniida
    - Orbiniidae
      - *Scoloplos armiger* (Müller)
  - Spionida
    - Spionidae
      - *Scolelepis fuliginosa* (Claparède)
    - Magelonidae
      - *Magelona papillicornis* Müller
  - Opheliida
    - Opheliidae
      - *Ophelia limacina*[1]
      - *Travisia forbesii* Johnston
  - Phyllodocida
    - Phyllodocidae
      - *Anaitides groenlandica* Örsted
      - *Anaitides maculata*
      - *Eumida sanguinea* Örsted
    - Polynoidae
      - *Harmothoe lunulata* (Delle Chiaje)[2]
    - Sigalionidae
      - *Sthenelais boa* (Johnston)
    - Nereidae
      - *Nereis pelagica* Lamarck
      - *Nereis diversicolor* (Örsted)
    - Goniadidae
      - *Goniada maculata* Örsted
    - Nephtydidae
      - *Nephtys caeca* (Müller)
      - *Nephtys cirrosa*[3] Ehlers
  - Terebellida
    - Pectinariidae
      - *Lagis koreni* Malmgren
    - Terebellidae
      - *Lanice conchilega* (Pallas)

APPENDIX III

- Arthropoda
  - Malacostraca
    - Cumacea[4]
      - *Cumopsis goodsiri*
      - Pseudocumidae
        - *Pseudocuma longicornis* (Bate)
        - *Pseudocuma gilsoni*
    - Isopoda
      - Cirolanidae
        - *Eurydice pulchra* Leach
    - Amphipoda[4]
      - Haustoridae
        - *Bathyporeia guilliamsonia* (Bate)
        - *Bathyporeia elegans* Watkin
        - *Pontocrates arenarius*
      - Atylidae
        - *Atylus swammerdami* (Milne-Edwards)
      - Gammaridae
        - *Gammarus locusta* Lamarck
        - *Marinogammarus* sp.
    - Decapoda
      - Hippolytidae
        - *Crangon crangon* (Lamarck)
      - Portunidae
        - *Carcinus maenas* (Lamarck)
- Mollusca[5]
  - Pelecypoda
    - Mytiloida
      - Mytilidae
        - *Mytilus edulis* Lamarck
    - Veneroida
      - Cardiidae
        - *Cerastoderma edule* (Lamarck)
      - Mactridae
        - *Spisula solida* (Lamarck)
      - Cultellidae
        - *Ensis siliqua* (Lamarck)
      - Tellinidae
        - *Tellina tenuis* da Costa
      - Donacidae
        - *Donax vittatus* (da Costa)
      - Veneridae
        - *Chamelea gallina* (Lamarck)
          - =*Venus striatula* (da Costa)
    - Pholadomyoida
      - Thraciidae
        - *Thracia phaseolina* (Lamarck)

Appendix III

Echinodermata
- Asteroidea
  - Forcipulata
    - Asteriidae
      - *Asterias rubens* Lamarck

Chordata
- Teleostomi
  - Percomorphi
    - Ammodytidae
      - *Ammodytes tobianus* Lamarck
  - Heterosomata
    - Pleuronectidae
      - *Limanda limanda* (Lamarck)
      - *Pleuronectes platessa* Lamarck

Notes

1. *Ophelia limacina* (Rathke)

Tebble (1952) did not recognise *O. limacina* from British waters but Hartmann-Schröder (1971) considered Tebble's *O. borealis* Quatrefages to be *O. limacina* and redefined the following species:

16-24 pairs of branchiae; 2 large anal papillae *O. limacina*

8-10 pairs of branchiae; 1 large anal papillae *O. rathkei*

On this basis my samples contained *O. limacina*

Appendix III

Notes (continued)

2. Harmothoë lunulata (Delle Chiaje)

Eleftheriou (pers. comm.) suggested that this may be an offshore species which I have confused with H. marphysae McIntosh. I have based my identification on Hartmann-Schröder (1971) whose figure (Abb. 13) and description (pp. 56-57) match my specimen closely.

3. Nephtys cirrosa Ehlers

These specimens originally identified as N. longosetosa based on Fauchald (1963). Fauchald did not describe N. cirrosa and on re-examination of preserved specimens from LTT1 (October 1979) I have re-classified all N. longosetosa as N. cirrosa after Hartmann-Schröder (1971). These may represent a mixed population. Clark et al. (1962) reported a mixed population of N. longosetosa and N. caeca from the West Sands, St. Andrews but noted the predominance of N. cirrosa on most other Scottish beaches.

4. Cumacean and Amphipod species as reported by Eleftheriou (pers. comm.).

5. Molluscan nomenclature after McKay and Smith (1979).

APPENDIX IV

Flume contruction

A free standing water channel, constructed of reinforced fibreglass with a return circuit of PVC pipe was used in all experiments (Appendix Figure II). This recirculating flume was filled with 100 l of fresh seawater obtained from the surface of settling tanks. The test section had a working cross section of 250 cm^2 (10 cm deep, 25 cm wide) and the length to width ratio of the channel was 4:1 (settling length and test section). The flow was produced by a DC shunt wound motor (Paravlux 1/4 h.p.) and variable speed gearbox turning a perspex propellor mounted on a brass shaft. The speed of flow was controlled with a thyristor DC controller (Parvalux) and measured by timing suspended particles near the bed. 100 PVC pipes (2 cm diameter x 10 cm long) served as a collimator and a 50 w aquarium heater and thermostat maintained the seawater at $12^{o}C$. The walls of the test section were composed of a plate glass view port and a black plastic background, both flush with the walls of the flume. The floor of the flume was spread with a 5 mm layer of sediment collected from Tentsmuir Beach (mean diameter 2.40 phi 190 um) to provide a roughness equivalent to the floor of the tidal channel (only where it was smooth, e.g. devoid of any other tubes or bedforms).

APPENDIX V

Particles of denatured egg albumen were prepared by rinsing 60 g of hard boiled egg white in distilled water and pressing it twice through a plastic mesh sieve (two sizes used: 0.5 mm and 1.0 mm). The particles were rinsed three times with distilled water on plastic mesh one phi grade smaller (0.25 mm or 0.5 mm) and then once through plastic mesh one phi grade larger (1.0 mm or 2.0 mm) onto the finer mesh to remove irregularly-sized particles. The residue was then rinsed thoroughly with filtered seawater and washed through a clean sieve of the original mesh size with 1.5 l of filtered seawater into suspension in a beaker. This procedure resulted in sub-spherical particles with grain sizes of 0.5-1.0 mm and 0.25-0.5 mm.

The most useful particles for visualization of fluid movement are large (particles >0.25 mm are easy to photograph) and neutrally buoyant. To successfully mimic the movement of small natural particles, it is necessary for the visualization particles to have comparable hydrodynamic characteristics; thus, they must have a density somewhat greater than seawater. In order to determine the appropriate size and density a theoretical approach was used as a precursor to extensive empirical measurement.

Two hydrodynamic characteristics widely used in studies of sediment transport and resuspension (terminal settling velocity and Shields threshold criterion) were calculated for spheres of egg albumen density immersed in seawater using curves constructed by Yalin (1972) and extended by Miller et al. (1977), (Table 6-1). The procedure for calculating theoretical settling velocity and Shields threshold criterion for novel conditions is described in detail in Miller and Komar (1977).

The particles produced by the method described above were not spheres but angular, sub-spherical shapes. This should reduce the accuracy of the predicted values, Baba and Komar (1981) reported that while grain roundness had no significant effect on settling velocities, non-spherical particles had a settling velocity lower than that of spheres. This listing of hydrodynamic characteristics (Table 6-1) is not intended as an accurate measure but rather as a preliminary guide to the mesh sizes of egg particles useful for mimicking natural particles.

APPENDIX TABLE I

Macrofauna counts for all can core samples from Tentsmuir Beach study area. Sample sites listed in left-hand column, see Appendix Figure I for key (P=May 1978, j=August 1978, i=October 1978, f=March 1979). Division classification and sample date in right hand columns, see key at bottom. Species key listed below.

Nl *Nephtys cirrosa*

Tt *Tellina tenuis*

Lc *Lanice conchilega*

Ol *Ophelia limacina*

Es *Eumida sanguinea*

Hl *Harmothoë lunulata*

Am *Anaitides maculata*

Dv *Donax vittatus*

Ss *Spisula solida*

Sa *Scoloplos armiger*

Cm *Carcinus maenas*

Cr *Crangon crangon*

Np *Nereis pelagica*

Me *Mytilus edulis*

Nc *Nephtys caeca*

Nd *Nereis diversicolor*

Tf *Travisia forbesii*

Vs (*Venus striatula*) *Chamelea gallina*

Ce *Cerastoderma edule*

Ar *Asterias rubens*

At *Ammodytes tobianus*

Sb *Stenelais boa*

Al *Amphiporas lactifloreus*

	NJ	Tt	Lc	Ol	Es	Hl	Am	Dv	Ss	Sa	Cm	Cr	Np	Me	Nc	Nd	Tf	Vs	Ce	Ar	At	Sb	Al	Other	D	DATE
AM	9	41	28	11	12	0	0	2	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	10	4.78
MS	11	30	163	6	15	1	1	0	0	0	0	1	0	2	1	1	0	0	0	0	0	0	0	0	01	4.78
MK	2	25	210	0	58	4	7	0	0	3	1	0	1	0	0	2	0	1	0	0	0	0	0	0	02	4.78
LX	12	48	104	8	18	2	0	2	6	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	01	4.78
PF	15	62	116	3	26	0	3	0	3	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	01	4.78
1p	14	60	89	12	5	1	2	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	01	5.78
1j	1	46	175	6	10	5	0	2	0	1	1	7	0	0	2	0	0	0	0	0	0	0	0	0	01	8.78
1i	20	51	145	2	26	5	5	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	03	10.78
1f	7	45	56	5	0	0	0	0	0	0	0	0	0	6	0	1	0	0	0	0	0	0	0	1	20	3.79
2p	12	75	65	4	4	1	0	0	5	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	01	5.78
2j	7	63	155	3	0	1	0	1	7	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	01	8.78
2i	14	80	201	4	41	2	3	0	0	0	6	0	3	0	0	0	0	0	0	0	0	0	0	0	03	10.78
2f	12	85	227	1	10	2	12	0	0	0	12	1	0	2	0	0	0	0	2	1	0	0	0	3	03	3.79
3p	6	50	28	10	3	0	1	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	11	5.78
3j	2	43	0	4	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	11	8.78
3i	7	71	5	2	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	22	10.78
3f	12	60	1	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	11	3.79
4p	5	36	42	8	4	1	1	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	01	5.78
4j	3	73	187	11	1	5	0	0	2	0	2	0	0	0	3	0	0	2	0	0	0	0	0	0	02	8.78
4i	7	58	147	13	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	02	10.78
4f	15	51	210	4	19	2	3	0	1	0	7	0	0	5	1	0	0	0	0	0	0	0	0	0	03	3.79
5p	6	49	91	4	4	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	02	5.78
5j	7	16	98	2	2	4	0	0	2	0	0	1	0	0	3	0	0	0	0	0	0	0	0	0	02	8.78
5i	5	39	126	2	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	02	10.78
5f	12	22	80	6	0	0	3	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	10	3.79
6p	5	81	49	11	4	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	01	5.78
6j	2	19	68	2	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	02	8.78
6i	10	28	255	5	4	1	3	0	0	0	2	3	3	0	0	0	0	0	0	0	0	0	0	0	02	10.78
6f	6	27	50	0	0	2	3	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	10	3.79
7p	5	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	5.78
7j	7	3	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	8.78
7f	5	0	1	1	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	33	3.79
8p	9	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	33	5.78
8j	5	2	6	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	8.78
8i	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	33	10.78
8f	7	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	33	3.79
9p	9	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	5.78
9j	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	8.78
9f	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	33	3.79
10p	10	9	3	0	0	0	0	1	3	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	33	5.78
10j	2	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	8.78
10i	4	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	33	10.78
10f	7	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	33	3.79
EBT1	11	41	163	0	9	2	5	0	1	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	01	3.79
EBT2	9	53	198	3	8	3	12	1	0	0	22	0	0	65	1	0	0	2	1	0	0	0	0	0	01	3.79
LTC1	12	40	4	12	0	0	0	0	0	0	0	0	0	120	0	0	0	0	0	0	0	0	1	0	10	4.79
LTC2	8	28	12	0	4	0	8	0	0	0	0	0	0	35	4	0	0	0	0	0	0	0	0	0	10	4.79
HD1	14	41	291	10	3	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	02	7.78
HD2	15	46	322	17	3	1	2	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	02	7.78
LTT1	15	12	77	1	7	0	10	1	0	2	0	15	0	150	0	0	0	0	0	0	0	1	0	0	01	10.79
LTC3	13	47	9	5	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	10.79

01	A-M	ALGAL LANICE MOUND	
02	L-F	LANICE FLAT	> ALGAL LANICE ASSOCIATION HIGH TUBE DENSITY
03	I	ISLET	
10	R	SMALL RIPPLE FIELD	
20	B	BEACH FACE	> TELLINA-LANICE ASSOCIATION MED TUBE DENSITY
11	P	POOL	
22	D-C	DRAINAGE CHANNEL	> NEPHTHYS ASSOCIATION LOW TUBE DENSITY
33	M-R	MEGARIPPLE FIELD	

$

APPENDIX TABLE II

Numbers and biomass (in g) of macrofauna from two $0.08m^2$ samples taken within high tube density sites in July 1978 (see Appendix Figure I for location of sites). Appendix II gives details of sample collection and treatment.

	HD1		HD2	
	#	g	#	g
Lanice conchilega				
Adult	33	3.76	102	9.66
Juvenile	258	0.71	220	1.12
Ophelia limacina	10		17	
Nereis diversicolor	0		0	
Nephtys cirrosa	14		15	
Eumida sanguinea	3		3	
Anaitides maculata	1		2	
Harmothoë lunulata	1		1	
Other Polychaetes	1		1	
Tellina tenuis	41			
Donax vittatus	1			
Spisula solida				
Ensis siliqua				
Cerastoderma edule				
Chamelea gallina				
Lanice	291	4.47	322	10.78
All other polychaetes	30	0.24	40	0.63
Bivalves	42	0.52	47	0.66
Total infauna	363	5.23	409	12.07
Total biomass ($g\ m^{-2}$)		65.38		150.88
Total biomass w/o Lanice ($g\ m^{-2}$)		9.50		16.12

APPENDIX TABLE III

Numbers and biomass of individual macrofauna species from samples taken along transect in May 1978 (see Appendix figure I for location of sites). Appendix II gives details of sample collected and treatment. Figure 5-5 plots the values for total biomass, Lanice biomass, bivalve biomass and polychaete biomass against the transect stations.

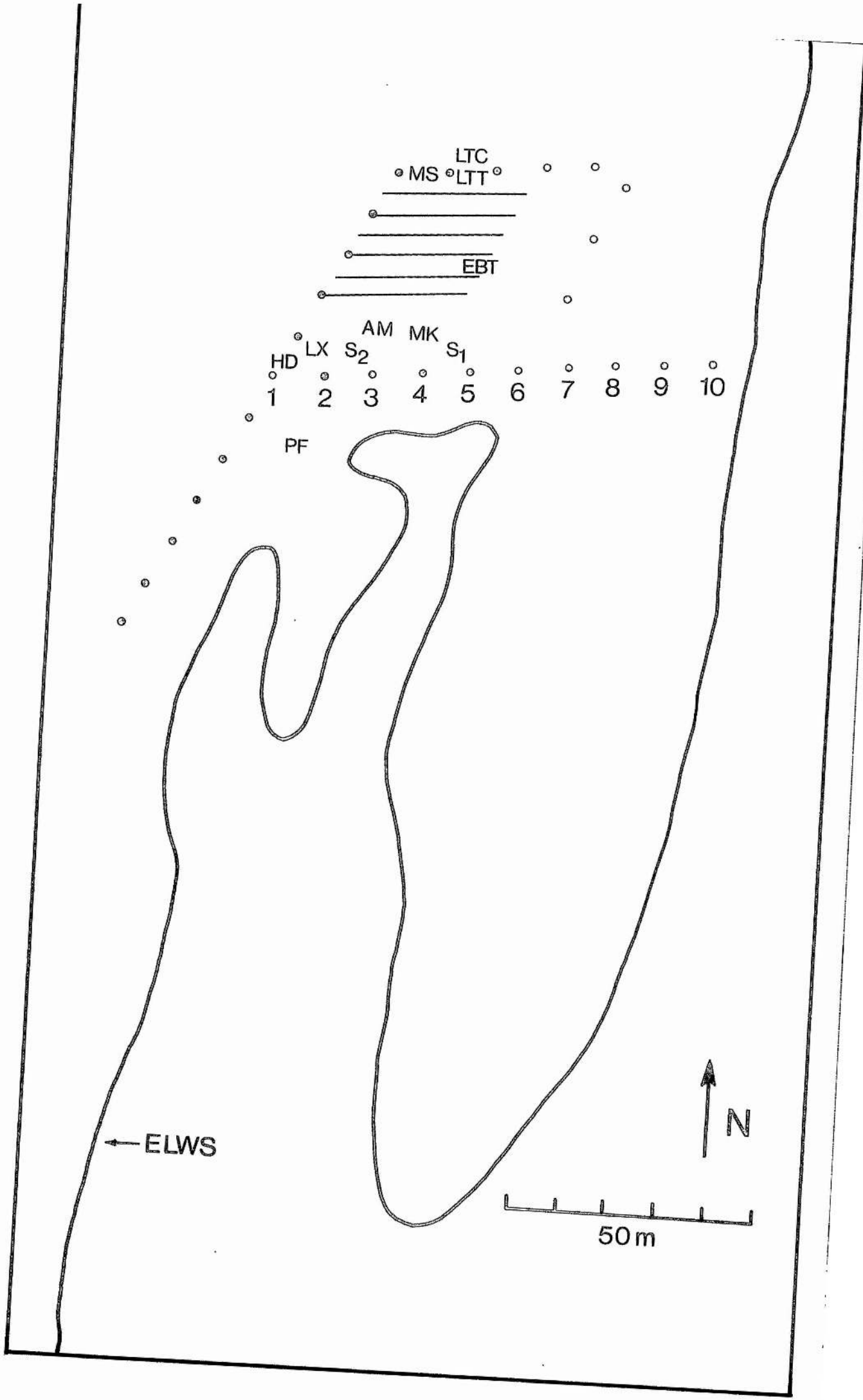
	1p		2p		3p		4p		5p	
	#	g	#	g	#	g	#	g	#	g
Lanice conchilega	89	2.75	65	2.22	28	1.02	42	1.35	91	2.91
Adult										
Juvenile										
Ophelia limacina	12	0.36	4		10	0.24	8		4	
Nereis diversicolor	1	0.66	1				1	0.82	1	0.74
Nephtys cirrosa	14		12		6		5		6	
Eumida sanguinea	5		4		3		4		4	
Anaitides maculata	11				1		1			
Harmothoë lunulata			1				1		2	
Other Polychaetes	3	0.76			3		1			
Tellina tenuis	60	0.48	75	0.77	50	0.31	36	0.32	49	0.44
Donax vittatus										
Spisula solida			5	0.26			1	0.03		
Ensis siliqua									1	0.91
Cerastoderma edule							1	0.67		
Chamelea gallina										
Lanice	89	2.75	65	2.22	28	1.02	42	1.35	91	2.91
All other polychaetes	46	1.78	22	0.23	23	0.39	21	1.10	16	0.78
Bivalves	60	0.48	80	1.03	50	0.31	38	1.02	50	1.35
Total infauna	196	5.01	167	3.48	101	1.72	101	3.47	157	5.04
Total biomass ($g\ m^{-2}$)		62.62		43.50		21.50		43.38		63.00
Total biomass w/o Lanice ($g\ m^{-2}$)		28.25		15.75		8.75		26.50		26.63

	6p		7p		8p		9p		10p	
	#	g	#	g	#	g	#	g	#	g
Lanice conchilega	49	1.49	0		0		0		3	0.09
Adult										
Juvenile										
Ophelia limacina	11	0.33					1			
Nereis diversicolor	1									
Nephtys cirrosa	5		5	0.03	9		9		11	
Eumida sanguinea	4									
Anaitides maculata										
Harmothoë lunulata	2									
Other polychaetes					1				2	
Tellina tenuis	81	1.13	10	0.06	8	0.05	1	0.001	9	
Donax villatus	1	0.08							1	
Spisula solida									3	2.16
Ensis siliqua										
Cerastoderna edule										
Lanice	49	1.49	0	0.00	0	0.00	0	0.00	3	0.09
All other polychaetes	23	0.51	5	0.03	10	0.05	10	0.06	13	0.09
Bivalves	82	1.21	10	0.06	8	0.05	1	0.001	14	2.26
Total infauna	154	3.21	15	0.09	18	0.10	11	0.06	30	2.44
Total biomass ($g\ m^{-2}$)		40.12		1.12		1.25	0.75			30.50
Total biomass w/o Lanice ($g\ m^{-2}$)		21.50		1.12		1.25	0.75			29.38

APPENDIX FIGURE I

Diagram of study area at Tentsmuir Beach showing grid system, transect and sample sites. Parallel lines are temporary transects used to count Eider browsing trances in March 1979 (see Section 5.3.3). Sample sites are listed below.

Site	Sample date	Sample		
AM	April 1978	4 can cores	faunal count	Preliminary survey
MS	April 1978	4 can cores	faunal count	Preliminary survey
MK	April 1978	4 can cores	faunal count	Preliminary survey
LX	April 1978	4 can cores	faunal count	Preliminary survey
PF	April 1978	4 can cores	faunal count	Preliminary survey
1-10	May 1978	4 can cores	faunal count	Transect
1-10	August 1978	4 can cores	faunal count	Transect
HD	July 1978	4 can cores	faunal count	High density sample
1-6,8,10	October 1978	4 can cores	faunal count	Transect
1-10	March 1979	4 can cores	faunal count	Transect
EBT	March 1979	4 can cores	faunal count	Eider browsing traces
LTC	April 1979	4 can cores	faunal count	Lanice transplant control
LTC	October 1979	4 can cores	faunal count	Lanice transplant control
LTT	October 1979	4 can cores	faunal count	Lanice transplant plot
1-10	August 1978	Sediment sample		Transect
1-10	April 1980	Sediment sample		Transect
S_1	April 1980	Sediment sample		
S_2	April1980	Sediment sample		


LTC
MS
LTT
EBT
AM
MK
HD
LX
S2
S1
1
2
3
4
5
6
7
8
9
10
PF
ELWS
N
50 m

APPENDIX FIGURE II

Free standing saltwater flume constructed from fiberglass reinforced with polyester resin used to produce repeatable flow conditions. The flume is an open channel design with a closed return circuit of standard PVC drain pipe. A D.C. motor was used to turn a plastic propellor mounted on a brass shaft via a belt and pulley system. The flow direction is indicated by arrows. The flume was supported on brick plinths and held against a wall with angle brackets.

Legend:

WL water level

H heater

T thermostat

Co collimator

Vp viewport

Sb sediment box

V vane

Pu pulley

M motor

P propellor

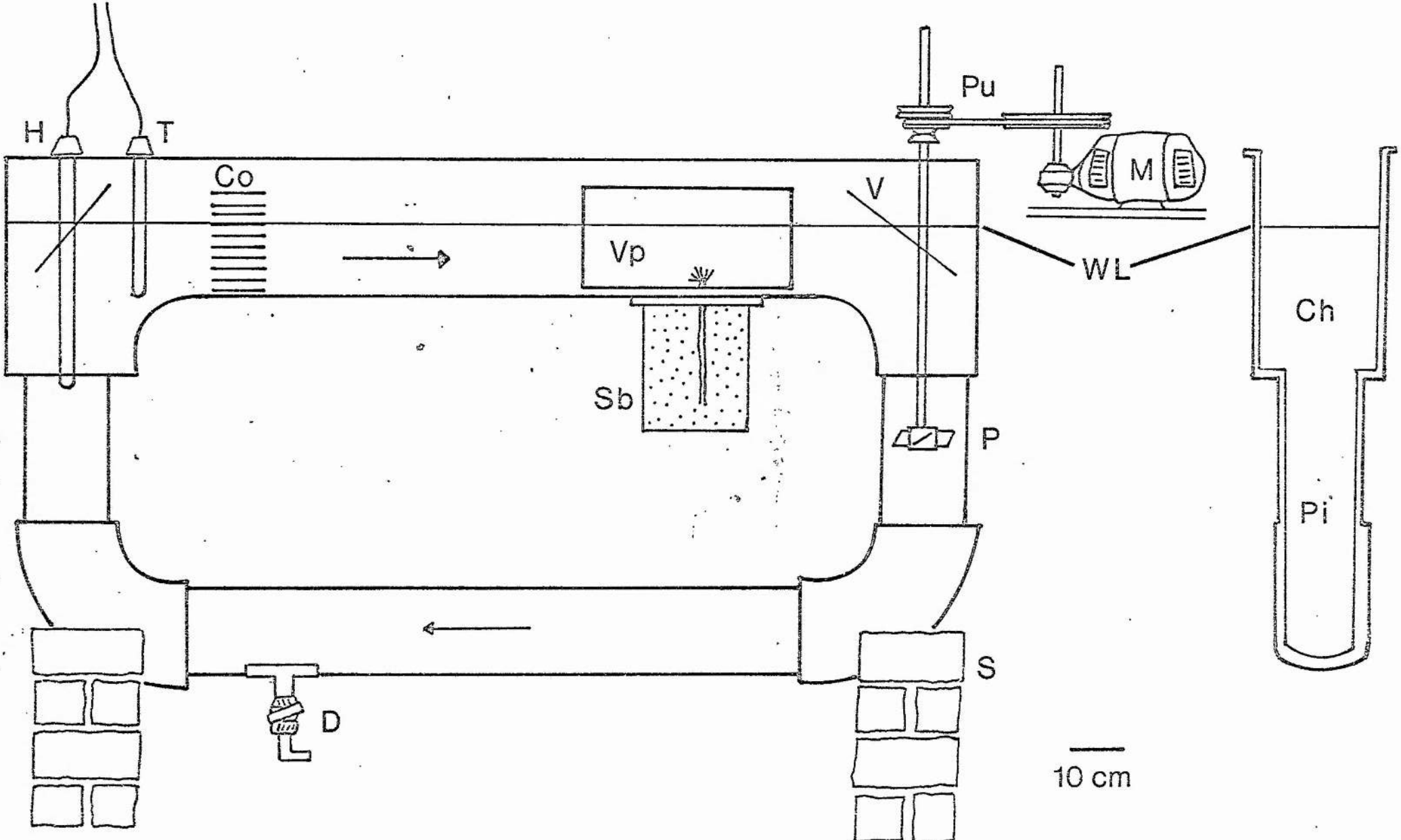
S support

D drain

Cross-section:

Ch channel

Pi pipe


H
T
Co
Vp
Sb
Pu
M
V
WL
Ch
Pi
P
S
D
10 cm

References

Alexander, W.B., B.A. Southgate and R. Bassindale (1935) Survey of the River Tees. Part 2. The estuary, chemical and biological. D.S.I.R., London (Tech. Pap. wat. Poll. Res. No. 5).

Allen, J.R.L. (1968) Current Ripples, North Holland Publ. Co., Amsterdam.

Allen, J.R.L. and P.F. Friend. (1976) Changes in intertidal dunes during two spring-neap cycles, Lifeboat Station Bank, Wells-next-the- Sea, Norfolk, England. Sedimentology 23:329-346.

Aller, R.C. (1980). Relationships of tube-dwelling benthos with sediment and overlying water chemistry. In: Tenore, K.R. and B.C. Coull, eds., Marine Benthic Dynamics Belle Baruch Library in marine science, 11:285-308.

Amoureux, L. (1960) Etude du pH de l'oxygenation et de la chlorinite dans le ruisseaux de l'Aber de Roscoff, en liaison avec le peuplement par divers polychetes. C. r. Acad. Sci. Paris 250:208-210.

Amoureux, L. (1968) Recherches écologiques sur les annélides polychètes du genre Nephtys. Arch. Zool. exp. gén. 109:69-77.

Arntz, W.E. (1980) Predation by demersal fish and its impact on the dynamics of macrobenthos. In: Tenore, K.R. and B.C. Coull, eds., Marine Benthic Dynamics. Belle Baruch Library in marine science, 11:121-149.

Baba, J. and P.D. Komar (1981) Settling velocities of irregular grains at low Reynolds numbers. J. sediment. Petrol. 51:121-128.

Baggerman, B. (1953) Spatfall and transport of Cardium edule L. Archs. néerl. Zool. 10:315-342.

Bailey-Brock, J.H. (1979) Sediment trapping by chaetopterid polychaetes on a Hawaiian fringing reef. J. Mar. Res 37:643-656.

Baxter, E.V. and L.J. Rintoul (1953) The Birds of Scotland, Oliver and Boyd, Edinburgh.

Bayne, B.L. (1964) Primary and secondary settlement in Mytilus edulis L. (Mollusca). J. Anim. Ecol. 33:513-523.

Beukema, J.J. (1976) Biomass and species richness of the macro-benthic animals living on the tidal flats of the Dutch Wadden sea. Neth. J. Sea Res. 10:236-261.

Bielakoff, J., D. Damas and J. Vovelle (1975) Histology and biochemistry of the glandular formations involved in the building of the tube of Lanice conchilega. Arch. Zool. Exp. Gen. 116:499-520.

Birkett, L. (1954) Standing crop, mortality and yield of a Mactra patch. ICES CM. North Sea Committee. No. 72.

van Blaricom, G.R. (1978) Disturbance, predation and resource allocation in a high-energy sublittoral sand-bottom ecosystem: experimental analysis of critical structuring processes for the infaunal community. Unpublished Ph.D. Thesis, University of California, San Diego.

Blatt, H., G. Middleton and R. Murray (1972) Origin of Sedimentary Rocks, Prentice-Hall, Inc., Inglewood Cliffs, New Jersey.

Blegvad, H. (1914) Food and conditions of nourishment among the communities of invertebrate animals found on or in the sea bottom in Danish waters. Rep. Dan. biol. Stn. 22:43-78.

de Boer, P.L. (1981) Mechanical effects of micro-organisms on intertidal bedform migration. Sedimentology 28:129-132.

Boersma, J.R. and J.H.J. Terwindt. (1981) Neap-spring tide sequences of intertidal shoal deposits in a mesotidal estuary. Sedimentology 28:151-170.

Bonner, W.N. (1972) The grey seal and common seal in European waters. Oceanogr. Mar. Biol. Ann. Rev. 10:461-507.

Bouma, A.H. (1969) Methods for the study of sedimentary structures, Wiley-Interscience, New York.

Braithwaite, C.J.R. (1973) Settling behaviour related to sieve analysis of skeletal sands. Sedimentology 20:251-262.

Brenchley, G.A. (1976) Predation detection and avoidance: ornamentation of tube-caps of Diopatra spp. (Polychaeta: Onuphidae). Mar. Biol. 38:179-188.

Brenchley, G.A. (1979) On the regulation of marine infaunal assemblages at the morphological level: a study of the interactions between sediment stabilizers, destabilizers and their sedimentary environment. Unpublished Ph.D. thesis, The Johns Hopkins University.

Bucher, W.H. (1919) On ripples and related sedimentary surface forms and their paleogeographic interpretations. Am.J.Sci. 47:149-210, 241-269.

Buhr, K.-J. (1976) Suspension feeding and assimilation efficiency in Lanice conchilega (Polychaeta). Marine Biology 38:373-383.

Buhr, K.-J. (1979) Eine Massensiedlung von Lanice conchilega (Polychaeta:Terebellidae) im Weser-Astuar. Veröff. Inst. Meeresforsch. Bremerh. 17:101-149.

Buhr, K.-J. and J.E. Winter (1977) Distribution and maintenance of a Lanice conchilega association in the Weser estuary (FRG) with special reference to the suspension-feeding behaviour of Lanice conchilega. In: Keegan, B.F., P.O. O'Ceidigh and P.J.S. Boaden (eds.) Biology of Benthic Organisms. 11th European Symp. on Marine Biology, Galway, Oct. 1976, pp. 101-113, Pergamon Press, Oxford.

Buller, A.T. (1975) Sediments of the Tay Estuary. II. Formation of ephemeral zones of high suspended sediment concentrations. Proc.R.Soc.Edinburgh 75B:65-89.

Buller, A.T., C.D. Green, and J. McManus. (1975) Dynamics and sedimentation: the Tay in comparison with other estuaries. In: Hails,J. and A.P. Carr (eds.) Nearshore sediment dynamics and sedimentation, pp.201-249, J.Wiley & Sons, Chichester.

Buller, A.T. and J. McManus. (1975) Sediments of the Tay Estuary. I Bottom sediments of the upper and upper middle reaches. Proc.R.Soc.Edinburgh

75B:41-64.

Buss, L.W. (1979) Habitat selection, directional growth and spatial refuges: why colonial animals have more hiding places. In: Larwood, G. and B.R. Rosen, eds., Biology and Systematics of Colonial Organisms, Systematics Ass. Spec. Vol. 11, pp. 459-497, Academic Press, London.

Carver, R.E. (ed.) (1971) Procedures in sedimentary petrology, Wiley Interscience, New York.

Caspers, H. (1938) Die Bodenfauna der Helgoländer Tiefen Rinne. Helgoländer wiss. Meeresunters. 2:1-112.

Cepek, P., and H.-E. Reineck (1970) Form und Enstehung von Rieselmarken im Watt- und Strandbereich. Senckenbergiana Marit. 2:3-30.

Chamberlain, C.K. (1971a) Morphology and ethology of trace fossils from the Ouachita Mountains, southeast Oklahoma. J.Paleontol. 45:212-246.

Chamberlain, C.K. (1971b) Biogenic mounds in the Dakota Sandstone of northwestern New Mexico. J.Paleontol. 45:641-644.

Chapman, G. (1965) The egg cocoons of Scoloplos armiger. Biol. Bull. 128:189-197.

Charlton, J.A. (1980) The tidal circulation and flushing capability of the outer Tay estuary. Proc.R.Soc.Edinburgh 78B:s33-s46.

Cheng, T.C. (1967) Marine molluscs as hosts for symbioses. In: Russell, F.S. (ed.), Adv. mar. Biol. 5, 424pp.

Chisholm, J.I. (1971) The stratigraphy of the post-glacial marine transgression in N.E.Fife. Bull.geol.Surv.G.B. 37:91-107.

Clark, R.B. (1960) Polychaeta, with keys to the British Genera. The Fauna of the Clyde Sea Area, Scottish Marine Biological Association, Millport.

Clark, R.B. (1962) Observations on the food of Nephtys. Limnol. Oceanogr. 7:380-385.

Clark, R.B. and A. Milne (1955) The sublittoral fauna of two sandy bays on the Isle of Cumbrae, Firth of Clyde. J. mar. biol. Ass. U.K. 34:161-180.

Clark, R.B. and E.C. Haderlie (1960) The distribution of Nephtys cirrosa and N. hombergii on the south-western coasts of England and Wales. J. Anim. Biol. 29:117-147.

Clark, R.B., J.R. Alder and A.D. McIntyre (1962) The distribution of Nephtys on the Scottish coast. J. Anim. Ecol. 31:359-372.

Clifton, H.E., R.E. Hunter, and R.L. Phillips (1971) Depositional structures and processes in the nonbarred high-energy nearshore. J.sediment.Petrol. 41:651-670.

Collinson, J.D. (1970) Bedforms of the Tana River, Norway. Geogr.Annlr. 52A:31-55.

Crawford, R.M. (1965) A multi-variate analysis of the development of dune slack vegetation in relation to coastal accretion at Tentsmuir, Fife.

J.Ecol. 54:729-743.

Crisp, D.J. (1979) Dispersal and re-aggregation in sessile marine invertebrates, particularly barnacles. In: Larwood, G. and B.R. Rosen (eds), Biology and Systematics of Colonial Organisms, Systematics Ass. Spec. Vol. 11, pp. 319-327, Academic Press, London.

Crisp, D.J. and A.J. Southward (1956) Demonstration of small-scale water currents by means of milk. Nature 178:1076.

Cullingford, R.A. (1972) Late-glacial and Post-glacial shoreline displacement in the Earn-Tay area and eastern Fife. Unpublished Ph.D. Thesis, University of Edinburgh.

Cunningham, J.T. and G.A. Ramage (1888) The Polychaeta Sedentaria of the Firth of Forth. Trans. R. Soc. Edinburgh 33:635-684.

Cuvier, G. (1836) Le Règne Animal distribué d'après son organisation pour servir de base à l'Histoire naturelle des animaux et d'introduction a l'anatomie comparée, Annelides, Paris, 54 pp.

Daly, J.M. (1972) The maturation and breeding biology of Harmothoë imbricata (Polychaeta:Polynoidea). Mar. Biol. 12:53-66.

Dalyell, J.G. (1853) Terebella littoralis seu arenaria, the sand mason. In: The powers of the Creator displayed in the Creation; or, various observations on life amidst the various forms of the humbler tribes of animated nature; with practical comments and illustrations - (a memoir of the author), 2:181-191, London.

Dare, P.J. and A.J. Mercer (1973) Foods of the Oystercatcher in Morecambe Bay, Lancashire. Bird Study 20173-184.

Davenport, D. (1953) Studies in the physiology of commensalism. IV. The polynoid genera Polynoë, Lepidasthenia and Harmothoë. J. mar. biol. Ass. U.K. 32:273-288.

Davies, J.L. (1964) A morphogenetic approach to world shorelines. Z.Geomorphol. 8:127-142.

Davis, R.A.,Jr. (ed.) (1978) Coastal Sedimentary Environments, Springer-Verlag, New York.

Dayton, P.K. and J.S. Oliver (1980) An evaluation of experimental analyses of population and community patterns in benthic marine environments. In: Tenore, K.R. and B.G . Coull (eds.), Marine Benthic Dynamics. Belle Baruch Library in marine science 11:93-120.

Dörjes, J., S. Gadow, H.-E. Reineck and I.B. Singh (1969) Die Rinnen der Jade (Südliche Nordsee). Sedimente und Makrobenthos. Senckenbergiana Marit. 1:5-62.

Donaldson, D. and S. Simpson (1962) Chomatichnus, a new ichnogenus, and other trace-fossils of Wegber Quarry. Liverpool Manchester geol. J. 3:73-81.

Dugán, P.J. (1981) The importance of nocturnal feeding in shorebirds: a consequence of increased invertebrate prey activity. In: Jones, N.V. and W.J. Wolff (eds.), Feeding strategies and survival of estuarine organisms. Marine Studies 15:251-260.

Dunthorn, A.A. (1971) Predation of cultivated mussel beds by eider. Bird Study 18:107-112.

Eagle, R.A. (1975) Natural fluctuations in a soft bottom benthic community. J. mar. biol. Ass. U.K. 55:865-878.

Eastwood, K.M. (1977) Some aspects of the sedimentology of the superficial deposits of the Eden estuary, Fife, Scotland. Unpublished Ph.D. Thesis, University of St Andrews.

Eckman, J.E. (1979) Small-scale patterns and processes in a soft-substratum intertidal community. J. Mar. Res. 37:437-457.

Eckman, J.E., A.R.M. Nowell and P.A. Jumars (1981) Sediment destabilization by animal tubes. J. Mar. Res. 39:361-374.

Edwards, R. and J.H. Steele (1968) The ecology of 0-group plaice and common dabs at Loch Ewe. I. Population and food. J. exp. mar. Biol. Ecol. 2:215-238.

Ehlers, E. (1875) Beiträge zur Kenntniss der Verticalverbreitung der Borstenwürmer im Meere. Zeits. wiss. Zool. 25:1-101.

Eleftheriou, A. and M.D. Nicholson. (1975) The effects of exposure on beach fauna. Cah. Biol. mar. 16:695-710.

Ettensohn, F.R. (1981) Crininicaminus haneyensis, a new agglutinated worm tube from the Chesterian of east-central Kentucky. J.Paleontol. 55:479-482.

Evans, S.M. (1971) Behavior in polychaetes. Q. Rev. Biol. 46:379-405.

Fager, E.W. (1964) Marine sediments: effects of a tube-building polychaete. Science 143:356-359.

Fauchald K. and P.A. Jumars (1979) The diet of worms: a study of polychaete feeding guilds. Oceanogr.Mar.Biol.Ann.Rev. 17:193-284.

Ferentinos, G. and J. McManus (in press) Nearshore processes and shoreline development in St Andrews Bay, Scotland, U.K. Sedimentology.

Folk R.L. (1968) Petrology of Sedimentary Rocks, Hemphills Bookstore, Austin.

Folk, R.L. and W.C. Ward (1957) Brazos River bar, a study in the significance of grain size parameters. J.sediment.Petrol. 27:3-27.

Frenkiel, L. and M. Mouëza (1979) Développement larvaire de deux Tellinacea, Scrobicularia plana (Semelidae) et Donax vittatus (Donacidae). Mar. Biol. 55:187-195.

Frostick, L.E. and I.N. McCave (1979) Seasonal shifts of sediment within an estuary mediated by algal growth. Est.Coast.Mar.Sci. 9:569-576.

Gibbs, P.E. (1968) Observations on the population of Scoloplos armiger at Whitstable. J. mar. biol. Ass. U.K. 48:225-254.

Gibson, R.N. (1973) The intertidal movements and distribution of young fish on a sandy beach with special reference to the plaice (Pleuronectes

platessa L.). J. exp. mar. Biol. Ecol. 12:79-102.

Gill, W.D. and P.H. Kuenen (1958) Sand volcanoes on slumps in the Carboniferous of County Clare, Ireland. Q.J.geol.Soc.London. 113:441-460.

Goldring, R. (1964) Trace fossils and the sedimentary surface in shallow marine sediments. In: van Straaten, L.M.J.U. (ed.) Deltaic and shallow marine deposits. Dev.Sedimentol. 1:136-143.

Goss-Custard, J.D. (1977a) The ecology of the Wash. III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). J. appl. Ecol. 14:721-739.

Goss-Custard, J.D. (1977b) Predator responses and prey mortality in redshank, Tringa totanus, and a preferred prey, Corophium volutator. J. Anim. Ecol. 46:21-35.

Goss-Custard, J.D., R.E. Jones and P.E. Newbery (1977a) The ecology of the Wash. I. Distribution and diet of wading birds (Charadrii). J. appl. Ecol. 14:681-700.

Goss-Custard, J.D., R.A. Jenyon, R.E. Jones, P.E. Newbery and R. le B. Williams (1977b) The ecology of the Wash. II. Seasonal variation in the feeding conditions of wading birds (Charadrii). J. appl. Ecol. 14:701-719.

Gray, J.S. (1974) Animal-sediment relationships. Oceanogr. Mar. Biol. Ann. Rev. 12:223-261.

Gray, J.S. (1981) The Ecology of Marine Sediments: Introduction to the structure and function of benthic communities, Cambridge University Press, Cambridge.

Green, C.D. (1974) Sedimentary and morphological dynamics between St Andrews Bay and Tayport, Tay estuary, Scotland. Unpublished Ph.D. Thesis, University of Dundee.

Green, C.D. (1975) Sediments of the Tay estuary. III. Sedimentological and faunal relationships on the southern shore at the entrance to the Tay. Proc.R.Soc.Edinburgh. 75(B):91-112.

Gregory, N. and W.S. Walker (1951) The effect of transition of isolated surface excrescences in the boundary layer. Rep. Memor. aero. Res. coun., Lond. 2779, 10p.

Griffiths, J.C. (1967) Scientific methods in the Analysis of Sediments, McGraw-Hill, New York.

Gutschick, R.C. and J. Rodriguez (1977) Late Devonian-Early Mississipian trace fossils and environments along the Cordilleran Miogeocline, western United States. In: Crimes,T.P. and Harper,J.C. (eds.) Trace Fossils 2. Geol.J.spec.issue. 9:195-208.

Hagmeier, A. (1951) Die Nahrung der Meerestiere. Handb. Seefisch. Nordeur. 1:86-242.

Hagmeier, A. and R. Kändler (1927) Neue Untersuchen im nordfriesischen Wattenmeer und auf den fiskalischen Austernbänken. Helgoländer wiss. Meeresunters. 16:1-90.

Hale, L.J. (1965) Biological Laboratory Data, Methuen, London.

Hannan, C.A. (1981) Polychaete larval settlement: correspondence of patterns in suspended jar collectors and in the adjacent natural habitat in Monterey Bay, California. Limnol. Oceanogr. 26:159-171.

Häntzschel, W. (1939) Brandungswälle, Rippeln und Fliessfiguren am Strande von Wangeroog. Nat.Volk.Frankfurt. 69:40-48.

Häntzschel, W. (1975) Miscellanea, Supplement 1, Trace fossils and problematica, 2nd Edn. In: Teichert, C. (ed.) Treatise on Invertebrate Paleontology, Geol.Soc.Am., Boulder, Colo. and Univ. of Kansas Press, Lawrence, Kansas.

Hartmann-Schröder, G. (1971) Annelida, Borstenwurmer, Polychaeta. Tierwelt Deutschlands 58:1-594.

Harden Jones, F.R. (1968) Fish Migration, Edward Arnold, London.

Harvey, P.H., J.S. Ryland and P.J. Hayward (1976) Pattern analysis in bryozoan and spirorbid communities. II. Distance sampling methods. J. exp. mar. Biol. Ecol. 21:99-108.

Hauser, B. (1973) Bestandsänderungen der Makrofauna an einer Station in ostfriesischen Watt. Jahresber. Forschungsstelle Norderney 1972 24:171-203.

Hayes, M.O. (1975) Morphology of sand accumulation in estuaries: an introduction to the symposium. In: Cronin, L.E. (ed.) Estuarine Research, Vol.II, Geology and Engineering, pp. 3-22, Academic Press, New York.

Heck, K.L., Jr. (1979) Some determinants of the composition and abundance of motile macroinvertebrate species in tropical and temperate turtlegrass (Thalassia testudinum). J. Biogeogr. 6:183-200.

Hill, G.W. and R.E. Hunter (1976) Interaction of biological and geological processes in the beach and nearshore environments, Northern Padre Island, Texas. In: Davis, R.A. and R.L. Etherington (eds.) Beach and nearshore sedimentation. Spec. Publ. Soc. econ. Paleontol. Mineral. Tulsa. 24: 169-187.

Holland, A.F., N.K. Mountford, M.H. Hiegel, K.R. Kaumeyer and J.A. Mihursky (1980) Influence of predation on infaunal abundance in Upper Chesapeake Bay, USA. Mar. Biol. 57:221-235.

Holme, N.A. (1950) Population-dispersion in Tellina tenuis da Costa. J. mar. biol. Ass. U.K. 29:267-280.

Holme, N.A. (1961) Notes on the mode of life of the Tellinidae (Lammellibranchia). J. mar. biol. Ass. U.K. 41:699-703.

Holme, N.A. and A.D. McIntyre (1971) Methods for the study of Marine Benthos, Blackwell Scientific Publ., Oxford.

Hommeril, P. (1962) Etude locale (Gouville-sur-mer Manche) de la retenue des sédiments par deux Polychetes sédentaires: Sabellaria alveolata et Lanice conchylega. Cah. Océanogr. 4:245-257.

Hommeril, P. and M. Rioult (1965) Etude de la fixation des sédiments

meubles par deux algues marines: Rhodothamniella floridula (Dillwyn) J.Feldm. et Microcoleus chtonoplastes Thur. Mar.Geol. 3:131-155.

Howard, J.D. (1972) Trace fossils as criteria for recognizing shorelines in stratigraphic record. In: Rigby, J.K. and W.K. Hamblin (eds.) Recognition of ancient sedimentary environments. Spec.Publ.Soc.econ.Paleontol.Mineral.Tulsa. 16:215-225.

Howard, J.D. (1975) The sedimentological significance of trace fossils. In: Frey, R.W. (ed.) The Study of Trace Fossils, pp. 131-146 Springer-Verlag, New York.

Howard, J.D. (1978) Sedimentology and trace fossils. In: Trace Fossil Concepts, Short course Soc.econ.Paleontol.Mineral. 5

Howard, J.D., C.A. Elders, and J.F. Heinbokel (1975) Estuaries of the Georgia coast, U.S.A.: Sedimentology and biology. V. Animal-sediment relationships in estuarine point bar deposits, Ogeechee River-Ossabow Sound, Georgia. Senckenbergiana Marit. 7:181-203.

Howard, J.D. and R.W. Frey (1975) Estuaries of the Georgia coast, U.S.A.: Sedimentology and biology. II. Regional animal-sediment characteristics of Georgia estuaries. Senckenbergiana Marit. 7:33-103.

Howard, J.D., T.V. Mayou and R.W. Heard (1977) Biogenic sedimentary structures formed by rays. J.sediment.Petrol. 47:339-346.

Howard, J.D. and H.-E. Reineck (1972) Georgia coastal region, Sapelo island, U.S.A.: Sedimentology and biology. IV. Physical and biogenic sedimentary structures of the nearshore shelf. Senckenbergiana Marit. 4:81-123.

Howells, W.R. (1964) The macrofauna of the intertidal soils of the Towy Estuary, Carmarthenshire. Ann. Mag. Nat. Hist. (13) 7:577-607.

Hughes, R.N. (1980) Predation and community structure. In: Price, J.H., D.E.G. Irvine and W.F. Farnham (eds.), The Shore Environment, vol. 2: Ecosystems, Systematics Ass. Spec. Vol. 17:699-728, Academic Press, London.

Hulscher, J.B. (1973) Burying-depth and trematode infection in Macoma balthica. Neth. J. Sea. Res. 6:141-156.

Hurlbert, S.H. (1971) The nonconcept of species diversity: a critique and alternative parameters. Ecology 52:577-586.

Inman, D.S. (1952) Measures for describing the size distribution of sediments. J.sediment.Petrol. 22:125-145.

Johnston, G. (1865) A catalogue of the British non-parasitical worms in the collection of the British Museum, London, 366 pp.

Jones, N.S. (1950) Marine bottom communities. Biol. Rev. 25:283-313.

Jones, N.V. and W.J. Wolff, eds. (1981) Feeding strategies and survival of estuarine organisms. Marine Science 15, Plenum Press, New York, 304 pp.

Jumars, P.A. and K. Fauchald (1977) Between-community contrasts in successful polychaete feeding strategies. In: Coull, B.C. (ed.), Ecology of Marine Benthos, Belle Baruch Library in marine science 6:1-20.

Jumars, P.A., A.R.M. Nowell and R.F.L. Self (1981) A simple model of flow-sediment-organism interaction. Mar. Geol. 42:155-172.

Kessler, M. (1963) Die Entwicklung von Lanice conchilega (Pallas) mit besonderer Beruchsichtigung der Lebensweise. Helgoländer wiss. Meeresunters. 8:425-476.

Khayrallah, N. and A.M. Jones (1975) A survey of the benthos of the Tay estuary. Proc.R.Soc.Edinburgh. 75B:113-135.

King, C.A.M. (1972) Beaches and Coasts, Edward Arnold, London, 2nd edn.

Klein, G. deV. (1970) Depositional and dispersal dynamics of intertidal sand bars. J.sediment.Petrol. 40:1095-1127.

Klein, G. deV. (1977) Clastic Tidal Facies, CEPCO, Champaign, Illinois.

Knight-Jones, E.W. (1951) Gregariousness and some other aspects of the setting behaviour of Spirorbis. J. mar. biol. Ass. U.K. 30:201-222.

König, D. (1948) Uber die Wohnweise einiger im Boden lebender Tiere im Wattenmeer. Verh. deutsch. Zoologen. Kiel, 1948:402-410, Leipzig.

Korringa, P. (1951) The shell of Ostrea edulis as a habitat. Arch. néerl. zool. 10:32-152.

Kühl, H. (1972) Hydrography and biology of the Elbe estuary. In: Barnes, H., (ed.), Oceanogr. Mar. Biol. Ann. Rev. 10:225-309, George Allen and Unwin, London.

Kuipers, B.R. (1977) On the ecology of juvenile plaice on a tidal flat in the Wadden Sea. Neth. J. of Sea Res. 11 (1):56-91.

Lande, R. (1973) Food and feeding habits of plaice (Pleuronectes platessa L.) in Borgenfjorden, North-Tröndelag, Norway. Norw. J. Zool. 21:91-100.

Lighthill, M.J. (1963) Boundary layer theory. In: Rosenhead, L. (ed.), Laminar Boundary Layers, pp. 46-113, Oxford University Press, Oxford.

Linke, O. (1939) Die Biota des Jadebusenwattes. Helgoländer wiss. Meeresunters. 1:201-348.

Macar, P. and C. Ek (1965) Un curieux phenomene d'erosion Fammeinnienne: Les "Pains de Gres" de Chambralles (Ardennes Belge). Sedimentology 4:53-64.

Maiklem, W.R. (1968) Some hydraulic properties of bioclastic carbonate grains. Sedimentology 10:101-109.

McCave, I.N. (1975) Vertical flux of particles in the ocean. Deep sea Res. 22: 491-502.

McIntosh, W.C. (1875) The marine Invertebrates and Fishes of St Andrews, Adam and Charles Black, Edinburgh.

McIntosh, W.C. and A.J. Masterman (1897) The Life Histories of the British Marine Food Fishes, Cambridge University Press, Cambridge.

McIntosh, W.C. (1922) Monograph of British Annelids Part II. The Polychaetes, vol. 4, Ray Society, London.

McIntyre, A.D. (1958) The ecology of Scottish inshore fishing grounds. I. The bottom fauna of East coast ground. Marine Research 1:3-24.

McIntyre, A.D. (1970) The range of biomass in intertidal sand with special reference to the bivalve Tellina tenuis. J. mar. biol. Ass. U.K. 50:561-575.

McIntyre, A.D. and A. Eleftheriou (1968) The bottom fauna of a flatfish nursery ground. J. mar. biol. Ass. U.K. 48:113-142.

McKay, D.W. and S.M. Smith (1979) Marine Mollusca of East Scotland, Royal Scottish Museum, Edinburgh.

McManus, J., A.T. Buller, C.D. Green (1980) Sediments of the Tay estuary. VI. Sediments of the lower and outer reaches. Proc.R.Soc.Edinburgh. 78B: s133-s153.

McMullen, R.M. and J.R.L. Allen (1964) Preservation of sedimentary structures in wet unconsolidated sands using polyester resins. Mar.Geol. 1:88-97.

Meadows, P.S. and J.I. Campbell (1972) Habitat selection by aquatic invertebrates. Adv. mar. Biol. 10:271-382.

Meyer, D.L. (1973) Feeding behaviour and ecology of shallow-water unstalked crinoids (Echinodermata) in the Caribbean Sea. Mar. Biol. 22:105-129.

Middleton, G.V. (1978) Facies. In: Fairbridge, R.W. and J. Bourgeois (eds.) Encyclopedia of Sedimentology, pp. 323-325, Dowden, Hutchinson & Ross, Stroudsberg, Pa.

Miller, M.C. and P.D. Komar (1977) The development of sediment threshold surves for unusual environments (Mars) and for inadequately studied materials (foram sands). Sedimentology 24:709-721.

Miller, M.C., I.N. McCave and P.D. Komar (1977) Threshold of sediment motion under unidirectional currents. Sedimentology 24:507-527.

Milliman, J.D. (1974) Marine Carbonates, Springer-Verlag, New York.

Mills, E.L. (1967) The biology of an ampeliscid amphipod crustacean sibling species pair. J. Fish. Res. Bd. Canada 24:305-355.

Milne, H. (1969) Eider biology. Report on B.O.U. Autumn Scientific Meeting. Ibis III, 278.

Milne, H. (1974) Breeding numbers and reproductive rate of eiders at the Sands of Forvie National Nature Reserve. Ibis 16:135-151.

Milne, H. and L.H. Campbell (1973) Wintering sea-ducks off the East coast of Scotland. Bird Study 20:153-172.

Mochizuki, M. (1961) Smoke observation on Boundary layer transition caused by a spherical roughness element. J. Phys. Soc. Japan 16:995-1008.

Moore, W.L. and F.D. Masch (1963) Influence of secondary flow on local scour at obstructions in a channel. Federal Inter-Agency Sedimentation

Conf. Proc., 1963, U.S. Dept. of Agriculture, Misc. Publ. 970:314-320.

Morkovin, M.V. (1964) Flow around a circular cylinder - a kaleidoscope of challenging fluid phenomena. Symposium on fully separated flows, ASME:102-118.

Morkovin, M.V. (1972) An approach to flow engineering via functional flow modules. Beiträge zur Strömungsmechanik, insbesondere zur Grenzschichttheorie Teil 2, Deutsche Luft- und Raumfahrt Forschungsbericht, 72-27, 1972, pp. 270-301.

Moss, A.J. (1972) Bed-load sediments. Sedimentology. 18:159-219.

Myers, A.C. (1970) Some palaeoichnological observations on the tube of Diopatra cuprea (Bosc): Polychaeta, Onuphidae. In: Crimes, T.P. and J.C. Harper (eds.) Trace fossils. Geol. J. spec. issue 3:331-334.

Myers, A.C. (1972) Tube-worms-sediment relationships of Diopatra cuprea (polychaeta:Onuphidae). Mar. Biol. 17:350-356.

Nio, S.D., J.H. van den Berg, M. Goesten, F. Smulders (1980) Dynamics and sequential analysis of a mesotidal shoal and intershoal channel complex in the eastern Scheldt (southwestern Netherlands). Sediment.Geol. 26:263-279.

Nowell, A.R.M and M. Church (1979) Turbulent flow in a depth-limited boundary layer. J. Geophys. Res. 84:4816-4824.

Oertel, G.F. (1972) Sediment transport of estuary entrance shoals and the formation of swash platforms. J.sediment.Petrol. 42:857-863.

Oertel, G.F. and J.D. Howard (1972) Water circulation and sedimentation at estuary entrances on the Georgia coast. In: Swift, D.J.P., D.B. Duane, O.H. Pilkey (eds.) Shelf Sediment Transport: Process and Pattern, pp. 461-498, Dowden, Hutchinson & Ross, Stroudsberg, Pa.

Ollivier, M.-T. (1969) Etudes des peuplements de Zostères, Lanice et Sabelles de la région Dinardaise. Tethys 1:1097-1138.

Pallas, P.S. (1766) Miscellanea Zoologica, quibus novae imprimis atque obscurae animalium species describuntur et observationibus iconibusque illustrantur. Hagae Comitum, XII and 224 p.

Perkins, E.J. (1974) The Biology of Estuaries and Coastal Waters, Academic Press, London.

Peterson, C.H. (1979) Predation, competitive exclusion and diversity in the soft-sediment benthic communities of estuaries and lagoons. In: Livingston, R.J., (ed.), Ecological Processes in Coastal and Marine Systems, Plenum Press, New York.

Pethon, P. (1967) Food and feeding habits of the common Eider. Contrib.Zool.Museum Univ.Oslo. 83

Pettijohn, F.J. and Potter, P.E. (1964) Atlas and glossary of primary sedimentary structures, Springer-Verlag, Berlin.

Pienkowski, M.W. (1981) How foraging plovers cope with environmental effects on invertebrate behaviour and availability. In: Jones, N.V. and W.J. Wolff, eds., Feeding strategies and survival of estuarine organisms.

Marine Science 15:179-192.

Player, P.V. (1971) Food and feeding habits of the common eider at Seafield, Edinburgh in winter. Wildfowl 22:100-106.

Pohlo, R.H. (1969) Confusion concerning deposit feeding in Tellinacea. Proc. malacol. Soc. London 38:361-364.

Pounder, B. (1971) Wintering Eiders in the Tay estuary. Scottish Birds 6:407-419.

Prys-Jones, O.E. (1973) Interactions between gulls and eiders in St. Andrews Bay, Fife. Bird Study 20:311-313.

Quatrefages, A. de (1865) Annélides et Gephyriens. Historie naturelle des AnneleE´s marins et d´eu douce. 2-3, 794 pp., Paris.

Rachor, E. and S.A. Gerlach (1978) Changes of macrobenthos in a sublittoral sand area of the German Bight, 1967-1975. Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer. 172:418-431.

Rasmussen, E. (1973) Systematics and ecology of the Isefjord marine fauna (Denmark) with a survey of the eelgrass (Zostera) vegetation and its communities. Ophelia 11:1-495.

Reading, H.G. (ed.) (1978) Sedimentary environments and facies, Blackwell, Oxford.

Reineck, H.-E. (1958) Wühlbau-Gefüge in Abhängigkeit von Sediment-Umlagerungen. Senckenbergiana Lethaea 39:1-24.

Reineck, H.-E. (1959) Werm eine Seehunds-Spur versteinerte. Natur u. Volk 89:47-53.

Reineck, H.-E. (1977) Natural indicators of energy level in Recent sediments: the application of ichnology to a coastal engineering problem. In: Crimes, T.P. and Harper, J.C. (eds.) Trace Fossils 2. Geol.J.spec.issue 9:265-272.

Reineck, H.-E., J. Dörjes, S. Gadow and G. Hertweck (1968) Sedimentologie, Faunenzonierung und Faziesabfolge vor der ostküste der inneren Deutschen Bucht. Senckenbergiana lethaia 49:261-309.

Reineck, H.-E. and I.B. Singh (1971) Der Golf von Gaeta (Tyrrhenisches Meer). III. Die Gefüge von Vorstrand and Schelfsedimenten. Senckenbergiana Marit. 3:185-201.

Reineck, H.-E. and I.B. Singh (1975) Depositional Sedimentary Environments, Springer-Verlag, New York.

Reise, K. (1978) Experiments on epibenthic predation in the Wadden Sea. Helgoländer wiss. Meeresunters. 31:55-101.

Rhoads, D.C. (1974) Organism-sediment relations on the muddy sea floor. Oceanogr. Mar. Biol. Ann. Rev. 12:263-300.

Rhoads, D.C. (1975) The paleoecologic and environmental significance of trace fossils. In: Frey, R.W. (ed.) The Study of Trace Fossils, pp. 147-160, Springer-Verlag, New York.

Rhoads, D.C. and L.F. Boyer (1982) The effects of marine benthos on physical properties of sediments, a successional perspective. In: McCall, P.L. and M. Trevesz (eds.), Contribution to Plenum Geobiology Series, vol. 2.

Rhoads, D.C., J.Y. Yingst and W.J. Ullman (1978) Seafloor stability in central Long Island Sound. I. Temporal changes in erodibility of fine-grained sediments. In: Wiley, M.L. (ed.), Estuarine Interactions, pp. 221-244, Academic Press, New York.

Rhoads, D.C. and D.K. Young (1970) The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. mar. Res. 28:150-178.

Rhoads, D.C. and D.K. Young (1971) Animal-sediment relations in Cape Cod Bay, Massachusetts. II. Reworking by Molpadia oolitica (Holothuroidea). Mar. Biol. 11:255-261.

Richardson, P.D. (1968) The generation of scour marks near obstacles. J. sediment. Petrol. 38:965-970.

Riemann-Zürneck, K. (1969) Sagartia troglodytes (Anthozoa). Biologie und Morphologie einer schlick bewohnenden Aktinie. Veröff. Inst. Meeresforsch. Bremerh. 12:169-230.

Risk, M.J. and Craig, H.D. (1977) Flatfish feeding traces in the Minas basin. J.sediment.Petrol. 46:411-413.

Robinson, A.H.W. (1975) Cyclical changes in shoreline development at the entrance to Teignmouth harbour, Devon, England. In: Hails, J. and A.P. Carr (eds.) Nearshore sediment dynamics and sedimentation, pp. 181-200, J. Wiley & Sons, Chichester.

Ronan, T.E., Jr. (1977) Formation and paleontologic recognition of structures caused by marine annelids. Paleobiology 3:389-403.

Roniewicz, P. (1970) Borings and burrows in the Eocene littoral deposits of the Tatra Mountains, Poland. In: Crimes, T.P. and J.C. Harper (eds.) Trace fossils. Geol.J.spec.issue 3:439-446.

Roper, A.T., V.R. Schneider and H.W. Shen (1967) Analytical approach to local scour. Pre-Congress Vol. 3, Proc. Paper No. C18, June, for XII Congress of IAHR, Fort Collins, Colorado.

Rubenstein, D.I. and M.A.R. Koehl (1976) The mechanisms of filter-feeding: some theoretical consideration. Am. Nat. 111:981-994.

Ruillier (1959) Etude bionomique de l'aber de Roscoff. Trav. Stat. Biol. Roscoff 10:5-350.

Sanders, H.L. (1956) Oceanography of Long Island Sound, 1952-1954. X. The biology of marine bottom communities. Bull. Bingham Oceanogr. Coll. 15:345-414.

Schäfer, W. (1972) Ecology and palaeoecology of marine environments Craig, G.Y. (ed.) Oliver & Boyd, Edinburgh.

Scheltema, R.S. (1974) Biological interactions determining larval settlement of marine invertebrates. Thalassia jugosl. 10:263-296.

Schlichting, H. (1960) Boundary Layer Theory, McGraw-Hill, New York.

Schneider, D. (1978) Equalisation of prey numbers by migratory shorebirds. Nature :271:353-354.

Sedney, R. (1973) A survey of the effects of small protuberances on Boundary-Layer flows. AIAA Journal 11:782-792.

Seilacher, A. (1951) Der Röhrenbau von Lanice conchilega (Polychaeta) Ein Beitrag zur Deutung fossiler Lebensspurren. Senckenbergiana Lethaea. 32:267-280.

Seilacher, A. (1953) Studien zur Palichnologie. Neues Jahrb.Geol.Palaeontol. Abhandlungen. 96:421-452.

Seilacher, A. (1964) Biogenic sedimentary structure. In: Imbrie, J. and N.D. Newell (eds.) Approaches to paleoecology, pp. 296-316, John Wiley & Sons, New York.

Selley, R.C. (1978) Ancient Sedimentary Environments, Chapman & Hall, London, 2nd edn.

Sengupta, S. (1966) Studies on orientation and imbrication of pebbles with respect to cross-stratification. J.sediment.Petrol. 36:362-369.

Shames, I.H. (1962) Mechanics of Fluids, McGraw-Hill, New York.

Simberloff, D. (1979) Nearest neighbor assessments of spatial configurations of circles rather than points. Ecology 60:679-685.

Simpson, S. (1970) Notes on Zoophycos and Spirophyton. In: Crimes, T.P. and J.C. Harper (eds.) Trace fossils. Geol.J.spec.issue 3:505-514.

Spärck, R. (1935) On the importance of quantitative investigations of the bottom fauna in marine biology. J. Cons. int. Explor. Mer. 10:3-67.

Spooner, G.M. and H.B. Moore (1940) The ecology of the Tamar estuary. VI. An account of the intertidal muds. J. mar. biol. Ass. U.K. 24:283-330.

Stecher, P.G. (ed.) (1968) Merck Index, 8th ed., Merck, Rahway, New Jersey.

Stephen, A.C. (1929) Studies on the Scottish marine fauna: The fauna of the sandy and muddy areas of the tidal zone. Trans. R. Soc. Edinburgh 56:291-306.

Stephen, A.C. (1930) Studies on the Scottish marine fauna. Additional observations on the fauna of the sandy and muddy areas of the tidal zones. Trans. R. Soc. Edinburgh 56:521-535.

Stephen, W.J. (1977) A one-man profiling method for beach studies. J.sediment.Petrol. 47:860-863.

Strathmann, R. (1974) The spread of sibling larvae of sedentary marine invertebrates. Am. Nat. 108:29-44.

Stripp, K. (1969) Die Assoziationen des Benthos in der Helgoländer Bucht. Veröff. Inst. Meeresforsch. Bremerh. 12:95-142.

Stripp, K. and S.A. Gerlach (1969) Die Bodenfauna im Verklappungsgebiet von Industrieabwässern nordwestlich von Helgoland. Veröff. Inst. Meeresforsch. Bremerh. 12:149-156.

Swennen, C. (1969) Crawling-tracks of trematode infected Macoma balthica (L.). Neth. J. Sea Res. 4:376-379.

Taghon, G.L., A.R.M. Nowell and P.A. Jumars (1980) Induction of suspension feeding in spionid polychaetes by high particulate fluxes. Science 210:562-564.

Tani, I., H. Komoda, Y. Komatsu and M. Iuchi (1962) Boundary-layer transition by isolated roughness. Aero. Res. Inst., Univ. of Tokyo, Rept. 375, pp. 129-142.

Tavener, J.H. (1963) Further notes on the spread of the eider in Great Britain. Brit. Birds 56:273-285.

Tebble, N. (1952) On three species of the genus Ophelia (Polychaeta) from British and adjacent waters. Ann. Mag. Nat. Hist. (12) 5:553-571.

Tebble, N.A. (1976) British Bivalve Seashells, H.M.S.O., Edinburgh, 2nd edn.

Teichert, C (1958) Concepts of facies. Bull. Amer. Assoc. Petrol. Geol. 42:2718-2744.

Thijssen, R., A.J. Lever and J. Lever (1974) Food composition and feeding periodicity of 0-group plaice in the tidal area of a sandy beach. Neth. J. Sea Res. 8(4):369-377.

Thorson, G. (1946) Reproduction and larval development of Danish marine bottom invertebrates. Meddelel. Komm. Danmarks Fisk-Havundersog. 4:1-523.

Thorson, G. (1966) Some factors influencing the recruitment and establishment of marine benthic communities. Neth. J. Sea Res. 3:267-293.

Thwaites, B. (ed.) (1960) Incompressible Aerodynamics, Clarendon Press, Oxford.

Tiberi, J. and J. Vovelle (1975) Dounées histochimiques sur la nature et la formation du tube larvaire chez Lanice conchilega Pallas, Polychète Terebellidae. Arch. Zool. exp. gén. 116:303-318.

Titman, C.W. and P.A. Davies (1976) The dispersal of young post-larval bivalve molluscs by byssus threads. Nature 262:386-387.

Trevallion, A. (1971) Studies on Tellina tenuis daCosta. III. Aspects of general biology and energy flow. J. exp. mar. Biol. Ecol. 7:95-122.

Trevallion, A., R.R.C. Edwards and J.H. Steele (1970) Dynamics of a benthic bivalve. In: Steele, J.H. (ed.), Marine Food Chains, pp. 285-295, Oliver & Boyd, Edinburgh.

Tritton, D.J. (1977) Physical Fluid Dynamics, Van Nostrand Reinhold, New York.

Tyler, P.A. and F.T. Banner (1977) The effect of coastal hydrodynamics on

the echinoderm distribution in the sublittoral of Oxwich Bay, Bristol Channel. Est. Coast. Mar. Sci. 5:293-308.

Virnstein, R.W. (1977) The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology 58:1199-1217.

Virnstein, R.W. (1978) Predator caging experiments in soft sediments: caution advised. In: Wiley, M.L. (ed.) Estuarine Interactions, pp. 261-273, Academic Press, New York.

Vogel, S. and M. LaBarbera (1978) Simple flow tanks for research and teaching. Bio. Science 28:638-643.

Walker, R.G. (ed.) (1979) Facies Models. Geoscience Canada Reprint Series 1, Geol. Assoc. Can. Publ., Toronto .

Warner, G.F. (1979) Aggregation in echinoderms. In: Larwood, G. and B.R. Rosen (eds.), Biology and Systematics of Colonial Organisms, Systematics Ass. Spec. Vol. 11:375-396, Academic Press, London.

Watkins, E.E. (1942) The macrofauna of the intertidal sands of Kames Bay, Milport, Buteshire. Trans. R. Soc. Edinburgh 60:543-561.

Watson, A.T. (1890) The tube-building habits of Terebella littoralis Jl. R. microsc. Soc., ser. 2, 10:685-689.

Watson, A.T. (1916) A case of apparent intelligence exhibited by a Marine tube-building Worm, Terebella conchilega. Jl. R. microsc. Soc., 1916, 253-256.

Wheeler, A. (1980) Fish-algal relations in temperate waters. In: Price, J.H., D.E.G. Irvine and W.F. Farnham (eds.) The Shore Environment, vol. 2: Ecosystems. Systematics Ass. Spec. Vol. 17:677-698, Academic Press, London.

Williams, D.J.A. and J.R. West (1975) Salinity distribution in the Tay estuary. Proc.R.Soc.Edinburgh 75B:29-39.

Wilson, D.P. (1948a) The larval development of Ophelia bicornis Savigny. J. mar. biol. Ass. U.K. 27:540-553.

Wilson, D.P. (1948b) The relation of the substratum to the metamorphosis of Ophelia larvae. J. mar. biol. Ass. U.K. 27:723-763.

Wilson, D.P. (1955) The role of microorganisms in the settlement of Ophelia bicornis Savigny. J. mar. biol. Ass. U.K. 48:387-435.

Wilson, W.H., Jr. (1979) Community structure and species diversity of the sedimentary reefs constructed by Petaloproctus socialis (Polychaeta:Maldanidae). J. mar. Res. 37:623-641.

Wilson, W.H., Jr. (1980) A laboratory investigation of the effect of a terebellid polychaete on the survivorship of nereid polychaete larvae. J. exp. mar. Biol. Ecol. 46:73-80.

Winter, J.E. (1973) The filtration rate of Mytilus edulis and its dependance on algal concentration, measured by a continuous recording apparatus. Mar. Biol. 22:317-328.

Wisely, B. (1960) Observations on the settling behaviour of larvae of the

tubeworm Spirorbis borealis Daudin (Polychaeta). Aust. J. mar. Freshwat. Res. 11:55-72.

Wohlenberg, E. (1937) Die Wattenmeer-Lebensgemeinschaften im Königshafen von Sylt. Helgoländer wiss Meeresunters. 1:1-92.

Wolff, W.J. (1973) The estuary as a habitat, an analysis of data on the soft-bottom macrofauna of the estuarine area of the rivers Rhine, Meuse and Scheldt. Zoologische verhandlingen, Leiden 126:1-242.

Wolff, W.J., M.A. Mandos and A.J.J. Sandee (1981) Tidal migration of plaice and flounders as a feeding strategy. In: Jones, N.V. and W.J. Wolff (eds.), Feeding and survival strategies of estuarine organisms. Marine Science 15:159-171.

Woodin, S.A. (1976) Adult-larval interactions in dense infaunal assemblages: patterns of abundance. J. mar. Res. 34:25-41.

Woodin, S.A. (1976) Stuctural heterogeneity and predation in an infaunal system. Am. Zool. 16:195.

Woodin, S.A. (1978) Refuges, disturbance, and community structure: a marine soft-bottom example. Ecology 59:274-284.

Wunderlich, F. (1970) Korngrössenverschiebung durch Lanice conchilega (Pallas). Senckenbergiana Marit. 2:119-125.

Wunderlich, F. (1971) Der Golf von Gaeta (Tyrrhenisches Meer). II. Strandaufbau and Stranddynamik. Senckenbergiana Marit. 3:135-183.

Wunderlich, F. (1972) Georgia coastal region, Sapelo island, U.S.A. Sedimentology and biology. III. Beach dynamics and beach development. Senckenbergiana Marit. 4:47-79.

Yalin, M.S. (1972) Mechanics of sediment transport, 1st edition, Pergamon Press, Oxford.

Yingst, J.Y. and D.C. Rhoads (1978) Seafloor stability in central Long Island Sound. II. Biological interactions and their potential importance for seafloor erodibility. In: Wiley, M.L. (ed.), Estuarine Interactions, pp. 245-260, Academic Press, New York.

Zdravkovich, M.M. (1977) Review of flow interference between two circular cylinders in varius arrangements. J. of Fluids Eng., Trans. ASME, 99:618-633.

Zenetos, A. (1980) Molluscan populations of the Eden estuary, Fife, and the use of numerical taxonomy methods to determine their distribution patterns. Unpublished M.Sc. Thesis, University of St. Andrews.

Ziegelmeier, E. (1952) Beobachtungen über den Röhrenbau von Lanice conchilega (Pallas) im Experiment und am natürlichen Standort. Helgoländer wiss.Meeresunters. 4:107-129.

Ziegelmeier, E. (1963) Das Makrobenthos in Ostteil der Deutschen Bucht nach qualitativen und quantitativen Bodengreiferuntersuchungen in der zeit von 1949-1960. Veröff. Inst. Meerforsch. Bremerh. 23:101-114.

Ziegelmeier, E. (1969) Neue Untersuchungen über die Wohnröhren-Bauweise von Lanice conchilega (Polychaeta, Sedentaria). Helgoländer